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The Social Life of Monkeys and Apes

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PLATE I

Photograph by F. W. Bon

AN ADULT MALE HAMADRYAS BABOON WITH HIS FEMALE

The Social Life of Monkeys and Apes

By

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WITH 24 PLATES

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TO

R. C. B.

CONTENTS

CHAP.		PAGE
	Author's Preface	xi
I.	Human Sociology and the Sub-Human Primates	1
II.	Mammalian Sociology	17
III.	Sexual Periodicity	32
IV.	The Breeding Season and Society	52
V.	The Physiology of the Reproductive Processes of Mammals other than Primates	68
VI.	The General Character of the Menstrual Cycle	83
VII.	The Morphology, Physiology, and Interpretation of the Menstrual Cycle	99
VIII.	The Œstrous Cycle and Behaviour	117
IX.	The Menstrual Cycle and Behaviour	137
X.	The Individual Within the Group	151
XI.	Apes and Monkeys in the Wild: General	172
XII.	Baboons in South Africa	193
XIII.	The Social Groups of Wild Apes and Monkeys	208
XIV.	The Hamadryas Baboon Colony	215
XV.	Dominance and the Liberation of Sexual Responses	232
XVI.	The Communal Life of the Baboon	248
XVII.	The Development of Social and Sexual Responses	265
XVIII.	Altruism and Society	292
XIX.	The Social Scale	306
	Bibliography	317
	Index of Animals	341
	Index of Authors and Subjects	349

LIST OF ILLUSTRATIONS

PLATE		PAGE
I.	An Adult Male Hamadryas Baboon with His Female	*Frontispiece.*
II.	Members of the Hamadryas Baboon Colony of Monkey Hill	14
III.	A Nursing Baboon and Her Baby	26
IV.	A Bachelor of Monkey Hill	40
V.	An Adult Female Hamadryas Baboon Grooming Her Overlord	54
VI.	One Bachelor Hamadryas Baboon Grooming Another	66
VII.	Two Overlords after the Removal of Their Females from Monkey Hill	78
VIII.	Male Hamadryas Baboons Drinking	94
IX.	A Group of Hamadryas Baboons Feeding	110
X.	Immature Male Baboons	126
XI.	The Bigamous Family Party of Monkey Hill	138
XII.	The Bigamous Family Party of Monkey Hill	148
XIII.	A Monogamous Pair of Baboons on Monkey Hill	166
XIV.	A Bachelor Baboon Eats a Melon, while an Immature Male Watches	186
XV.	A Young Baboon with Filled Cheek-Pouches	206
XVI.	A Male Baboon Eats Macaroni, His Female Making No Attempt to Secure Any	218
XVII.	Male Baboons Fighting—One Against All	226
XVIII.	A Male Hamadryas Baboon "Threatening"	240
XIX.	The Baby Baboon's Movements Controlled by Its Mother	250
XX.	A Young Female Baboon and the Bachelor Who had Attached Himself to Her Parents	260

PLATE PAGE

XXI. A Nursing Female Baboon and Her Overlord . . 270

XXII. The Baby Baboon Beginning to Walk . . . 282

XXIII. The Baby Baboon Beginning to Climb . . . 290

XXIV. A Female Baboon, with Her Dead Baby in Her Arms, Being Groomed by Her Overlord . . . 300

PREFACE

THIS book is the somewhat unexpected outcome of a paper read in February, 1929, before the Anthropological Society of University College, London, and subsequently published in *The Realist* (July, 1929). I was unprepared—since my own curiosity about the social behaviour of monkeys and apes had been aroused mainly through encounters with wild baboons in South Africa—for the ready interest shown in my observations, but the opinions expressed by Professor G. Elliot Smith, F.R.S., Dr. W. J. Perry and Professor B. Malinowski strengthened my own belief that the subject was relevant to anthropology and stimulated me to pursue it further. The opportunity of doing this was provided by my association with the Zoological Society of London. A study of its rich collection of monkeys and apes was greatly facilitated by the encouragement and indulgence of the Society's Prosectorial Committee, and especially of Sir Peter Chalmers Mitchell, F.R.S., the Society's Secretary. Aided by grants both from this Society and from the Royal Society of London, I was also able, in the early part of 1930, to revisit South Africa to collect anatomical material and once again to make observations on baboons in their natural habitat.

This volume embodies the results of my investigations. I do not claim to have given a complete account of the social lives of the animals which I studied, but, so far as I could, I have considered all the available and relevant facts. My own observations have been made without, I hope, anthropomorphic bias, and my interpretations have been weighted with no more than the insistence of the facts themselves. I have approached the subject from the deterministic point of view of the

physiologist, treating overt behaviour as the result or expression of physiological events which have been made obvious through experimental analysis. In doing this I am fully aware that others might wish to regard the data from an opposite angle.

I am deeply indebted to Professor G. Elliot Smith for his continuous interest in my work. To him, to Professor A. G. Tansley, F.R.S., to Professor J. P. Hill, F.R.S., Professor Lancelot Hogben and to Dr. A. S. Parkes, I owe thanks for many criticisms and suggestions. For permission to publish the pathological data recorded in Chapter XIV, I am indebted to Sir Peter Chalmers Mitchell, and to Colonel A. E. Hamerton, pathologist to the Zoological Society. My colleagues both of this Society and of the Institute of Anatomy, University College, have helped me in many ways. I am especially grateful to Dr. R. Lythgoe and to Dr. Katharine Tansley, who kept a record of the Zoological Society's colony of Baboons during my absence in South Africa last year, and to Miss Margaret Gardiner, who assisted me greatly in the preparation of this book. Mr. J. E. Saunders, Mr. F. W. Bond, and Herr Heinz Heck very kindly lent the photographs from which the plates were prepared.

S. ZUCKERMAN.

CHAPTER I

HUMAN SOCIOLOGY AND THE SUB-HUMAN PRIMATES

MONKEYS and apes had attracted human interest long before Hoppius, a naturalist of the eighteenth century, advised posterity that "it would lead not a little to Philosophy, if one were to spend a day" with apes "exploring how far human wit exceeds theirs, what distance lies between Brutish and rational discrimination."* His was a somewhat enterprising suggestion, since the only available information on which he could have based such an opinion consisted entirely of anecdotes whose apparent object was to show not how far removed apes are from men but, on the contrary, how subtly they behave and how often their behaviour can be described in terms which are found adequate to describe our own. But perhaps this utterance merely reflected his acceptance of Cartesian principles; or it may be that he doubted the accuracy of the literature on monkeys and apes—a literature so attractively unreal that any scientific discussion of the ways of the lower primates must seem commonplace in comparison. It is, indeed, not surprising that the anecdotal zoological literature of the late eighteenth and the early nineteenth centuries led students of human society further and further into the belief that close observation of the ways of apes and monkeys might reveal truths that would form a foundation for a study of the beginnings of human social behaviour.

Buffon,[56] and the Rev. W. Bingley,[44] as well as Griffith, Hamilton Smith, and Pidgeon,[128]† writing in the

* Quoted from Yerkes and Yerkes.[395]

† The editors of an English edition of Cuvier's *Animale Regnum*.

eighteenth and early nineteenth centuries, give delightful accounts of the lives and characters of monkeys and apes, and have spun around the subject a web of romance from which it has not yet been freed. The Rev. W. Bingley tells of troops of "Oran Otans", four thousand strong, living on the wooded banks of the river Gambia; and Buffon claims that "this animal is as tall and as strong as man, and as desirous of the female sex". We are told that it uses stones to attack its enemies, and sleeps in trees, where it forms a kind of arbour to shelter from the weather. The same animal is also said to display a charming modesty. Bontius, who was head physician at Batavia in 1650, viewed with admiration some orangs walking erect, and among them a female "which seemed to have an idea of modesty, by covering with her hand a particular part of her body, from the sight of men whom she was not acquainted with".* M. Pallavicini, who was stationed at Batavia about a century later, kept two orangs, a male and a female, "which were extremely mild and gentle". If "the female was attentively looked at by any person, she would throw herself into the arms of the male, and hide her face in his bosom". † Although modest, apes nevertheless appear to be alarmingly ferocious, showing no mercy to luckless negroes who happen to cross their paths. They kill only the men, in their passion abducting the women, "which they keep with them for the pleasure of their company, feeding them very plentifully all the time."[56] It is also said that during the breeding season male apes are almost equally considerate to their own females and offspring, to whom they surrender their arbours, and Battel, a Portuguese traveller, tells us—although Bingley found this hard to believe—that when an ape dies its fellows cover up the body with great branches of trees.

The romance continues around the exploits of monkeys, who, we learn, live in much larger troops than do apes.

* Quoted from Buffon.[56] † Bingley.[44]

"Some naturalists have been credulous enough to believe that they form a sort of republic, in which a great degree of subordination is kept up; that they always travel in regular order, conducted by chiefs, the strongest and most experienced animals of their troop; and that, on these occasions, some of the largest Monkeys are likewise placed in the rear, the sound of whose voices immediately silences that of any of the others which happen to be too noisy. The negroes of Africa believe that these animals are a vagabond race of men, who are too indolent to construct habitations or to cultivate the ground." [44]

But even human renegades must suffer the serpent. The monkey, says a traveller cited by Buffon,

"has it in his power to be master of the forest, for there are neither tygers nor lyons which can dispute the possession with it: the chief animal it has to fear, and which attack them both night and day is the snake. There are some snakes in those forests of a prodigious size, which wind up the trees where the monkies reside, and when they happen to surprise them sleeping, swallow them whole before the little animals have time to make a defence."

Although not as swift and stealthy as the serpent, man is an equally formidable enemy, whose attacks, it is said, stimulate monkeys to display great mutual solicitude. If one is shot and falls to the ground, "all the rest set up a dismal and tremendous howl", and if one is wounded his fellows will seize him and carry him well out of the reach of the enemy.[44] M. Tavernier tells how, when travelling in the East Indies with the "English president", the latter was so much amused by the large monkeys playing in the trees around him that he desired to shoot one. Undeterred by the advice of his attendants, he did so.

Immediately all the remaining monkeys "to the number of sixty or upwards, descended in fury, and as many as could, leaped upon the president's coach, where they would soon have strangled him, had not the blinds been immediately closed, and the number of attendants so great as to drive them off. They

however continued to run after the servants, for at least three miles from the place where their companion was slain." *

Delightful accounts are given of the howler monkeys. Buffon quotes Marcgrave's report and describes them as assembling every evening and morning in the woods, when one of them climbs above the others, and with a gesture invites his fellows to seat themselves around him. As soon as they are all seated,

> "he begins an oration with so quick and loud a voice, that, at a distance, it might be imagined they were all making a noise together. During the whole discourse the rest keeps a profound silence, and when it is ended, he makes signal to the rest to answer him, and immediately they all set up a cry together, till such time as by another sign with his hand, he orders them to be silent: when they are immediately obedient and quiet. Then the first renews his discourse, or his song, which, when finished, and the others have paid the utmost attention to, the whole assembly breaks up and separates."

It is not surprising to learn that animals with such a flair for social organization are capable of acts of lofty altruism. As soon as a howler monkey is wounded, writes Oxmelin, an author quoted by Buffon, its fellows gather round, and place their fingers in the wound,

> "as if they were desirous of sounding its depth. If the blood then flows in any quantity, they keep it shut up, while others get leaves, which they chew and thrust into the orifice. I can affirm having seen this circumstance several times with admiration."

The early zoological writers found little to admire in the ways of baboons. Thus Bingley states that they are "as tall as men, have long faces, sunken eyes, and are otherwise extremely disgusting", and Griffith, Hamilton Smith and Pidgeon describe them as "by far the most brutal, the most ferocious, the most vicious, and the most disgusting" of all apes and monkeys.

* Quoted from Bingley.[44]

Reports made about the beginning of the nineteenth century relate that immense troops of Chacma baboons may be encountered in the mountains near the Cape of Good Hope. When approached they "set up an universal and horrible cry for a minute or two, and then conceal themselves in their fastnesses, and keep a profound silence".[44] They make travelling very dangerous, sitting insolently on the tops of their rocks, from which they roll down stones of immense size. Robert Lade, who is quoted by the Rev. W. Bingley, was so impressed by the size of these baboons that he was surprised to learn that they were neither ferocious nor dangerous. A member of his party levelled a gun at a very large specimen that was sitting at the top of a tree.

> "This kind of menace, of which the animal, perhaps, recollected his having sometimes seen the consequences, terrified him to such a degree that he fell down motionless at our feet, and we had no difficulty in seizing him. But, when he recovered from his stupor, it required all our dexterity and efforts to keep him. We tied his paws together, but he bit so furiously, that we were under the necessity of binding our handkerchiefs over his head."

A baboon observed by Buffon was

> "insolently lascivious, and satisfied its strong desires in public. It seemed also to make a parade of its nakedness, presenting its posteriors oftener to the spectators than its head; but it was particularly impudent in the presence of women, and plainly showed its immoderate desires before them by an inexpressible lascivity. The magot, and some others of the monkey kind, have likewise the same strong inclinations, but as they are less in size, and not so petulant, they were more easily corrected; whereas, the baboon is not only an incorrigible animal, but intractable to the utmost degree."

The Wanderoo monkey also has a "strong passion" for the female sex. Buffon describes these animals as being extremely ferocious, and writes that according to Forbin they

"principally attack women, and often, after having greatly injured them, finish their cruelty by strangling. Sometimes they even come to their houses; but the Macaroes, who are very jealous of their wives, take care to prevent their entrance into their habitations; and the females not liking (as the chevalier humorously relates) either the manners or the figure of the paltry gallants, boldly stand on their defence, and with clubs, or whatever other arms they can provide, instead of answering their caresses, oblige their ugly suitors to retract, not, however, before they have damaged or plundered everything they can lay their hands on."

Throughout the literature one reads accounts of monkeys who go in a body to attack gardens or plantations, and who, in spite of the care that is taken to prevent their raids, are usually successful. It is said that before they begin their plunder, they invariably send one of their party to some prominent point, in order to warn the others of any interruption. The sentinel remains on guard throughout the raid and, if he perceives any human being approach, gives a loud bark, whereupon the rest of his troop immediately escape and take to the trees, carrying their booty with them. They are said to do incalculable injury to the orchards and crops, tearing down and destroying far more than they eat or carry away.

Buffon's account of the pillaging exploits of baboons is a delightful romance. He writes that the baboons

"generally keep together in companies, and sally forth to commit their depredations on the neighbouring vineyards, or orchards. 'As they are extremely fond of grapes, apples, and ripe fruit, they assemble together in great numbers, and proceed on their enterprize with previous deliberation. The dogs who are set to watch, do not easily conquer these animals, as they are extremely agile, and make dexterous use of their teeth and claws. On these occasions, a part of them enter the inclosure, while one of the company stands centinel; the rest stand without the fence, a small distance from each other, and form a line, reaching all the way from the inclosure to the rendezvous without, which is generally in some craggy mountains. Every thing being thus disposed, the plunderers within

the orchard throw the fruit to them without as fast as they can gather it; or, if the wall or hedge be high, to those that sit at the top, and these hand the plunder to those next their side. Thus, the fruit is pitched from one to another all along the line, till it is safely deposited at their headquarters: they catch it as ready as the most skilful tennis-player can a ball; and, while the business is going forward, which they conduct with great expedition, a most profound silence is observed among them. The centinel during this whole time continues upon the watch, extremely anxious and attentive; but, if he perceives any one coming, he instantly sets up a loud cry, and at this signal the whole company scamper off.' "

If reports are to believed, monkeys have triumphed in quite different encounters with human beings. A chronicler of the deeds of Alexander the Great relates that one night his soldiers happened to encamp on a mountain on which lived a large number of monkeys. Early next morning they saw from afar what appeared to be an immense army, approaching as if to give battle. Neither Alexander nor his officers could understand who the enemy might be, since they had already subdued all the princes of the country. Nevertheless, the alarm was immediately given, and soon the whole Macedonian army was drawn up in battle array. A captive prince was asked for his opinion, and shown the approaching enemy. He immediately recognized them as monkeys, and "the Macedonians were not a little chagrined that they should have been such fools as to mistake a troop of these imitative animals for a band of armed men".[44] They need not have been so chagrined, for another story relates how a band of soldiers was repulsed in South Africa by a troop of baboons.

In 1810, according to Lieutenant Schipp,* a baboon, one of a pack that lived in the rocks above Simonstown, entered the barracks and made off with some clothes. A party of twenty men, under an officer, was detailed to recover the stolen property, and a circuit was made to cut

* See Romanes.[298]

off the baboons from the caves in which they always took cover. Unfortunately, however, these tactics were forestalled and, according to the report, fifty baboons were detached to guard the entrance to the caves, while the rest, acting under the orders of an old grey-haired animal who was recognized as a frequent visitor to the barracks, started collecting large stones and other missiles. Unperturbed by these preparations, the soldiers rushed on to the attack. But in vain. For, at a scream from the leader, the enemy proceeded to hurl down such big stones that they were forced to retreat.

Thus apes and monkeys leave a trail of fantasy in their passage from one traveller's tale to another. Robert and Ada Yerkes seem to discount unduly the purely literary qualities of these early zoological writings when they state, "we have been deeply and unfavourably impressed by the uncritical copying, quoting, or paraphrasing of author by author. . . . As one contemplates the utter wastefulness and the negative intellectual value of this procedure, one is depressed."[395] The contemplation of the sociological generalizations of some too credulous writers perhaps provides better cause for depression. Only too often have anecdotal accounts, similar to those quoted in the preceding paragraphs, been made the basis for speculation about human social origins.

It is now generally recognized that anthropomorphic preoccupations do not help the critical development of knowledge, either in fields of physical or of biological inquiry. Gods had to be banished from the skies before it could be seen that the movements of the stars conformed to mathematical laws. The emotions of the moth had to be disregarded before the nature of its

reactions to light stimuli could be scientifically explained. But although this principle has been accepted in most fields of science, mammalian sociology has developed without any real regard for questions concerning the validity of anecdotal and anthropomorphic evidence, and, indeed, has seldom been discussed on its own merits or approached except in its relation to problems of human sociology.

In this respect mammalian sociology has been less fortunate than the study of animal or comparative psychology, which in the main is concerned with the "intelligence" and "learning" capacity of animals. This statement should not be taken to imply that there is any real distinction between the study of social behaviour and that of individual behaviour; only that it is found convenient to consider them separately. When the impetus given to biological inquiry by Darwin's exposition of the evolutionary hypothesis made them prominent subjects for discussion, both these aspects of mammalian behaviour were at first considered together, and there accumulated a wealth of literature to fill the Cartesian gulf separating man from the beasts, and proving the continuity of mind and society through the world of living organisms. The Darwinian period, in which animal behaviour as a distinct study was born, was one in which anthropomorphic interpretation flourished. Anecdotes were regarded in the most generous light, and it was believed that many animals were highly rational creatures, possessed of exalted ethical codes of social behaviour.

The gap between Darwinian animal psychology and modern comparative psychology is wide. In 1879, Lindsay, a London physician belonging (as Warden [369] writes in his essay on comparative psychology) to a small group of conservative psychologists, published a work, in two volumes, on animal behaviour. He states in his introduction that he is attempting "to *outline* the subject of *Mind in the Lower Animals*, to illus-

trate their possession of the *higher mental faculties as they occur in man*, of *reason* as contradistinguished from mere *instinct*". His method is anecdotal, and he naïvely tells his readers that he

> "derived much information from children, school-girls, young ladies, elderly ladies, farmers' wives, and other ladies who, with no bias or prejudice, no theories or speculations to support or to disturb them, told truthfully what they were in the habit of observing in their home pets or household retainers."

Yet Lindsay claims to "have been trained to separate fact on the one hand, from *fiction*, and from *inference* based upon observation, on the other".[232]

With the publication of Loeb's[233] tropism theory in 1890, a reaction against the psychological method typified by the foregoing passage set in. Loeb was not particularly concerned with the activities of mammals, but his insistence on the mechanical character of the responses of lower organisms struck a hard blow at the custom of "humanizing" behaviour. Lloyd Morgan[262] also exerted a powerful influence about the same time in encouraging the collection of controlled psychological observations. The experimental method of the study of mammalian behaviour was started soon afterwards by Thorndike.[354] Since 1900, experimental investigation has been completely divorced from anecdotal "psychology", which survives to-day mainly in books of "nature study" written for children, and in letters to the Press.

Until 1890, the study of the social behaviour of mammals developed hand in hand with the study of their "intelligence", and both subjects were usually treated in the same books. Perhaps the best-known purely anecdotal sociological work of this period is Kropotkin's *Mutual Aid*, first published as essays in 1890,[223] and later reprinted in the form of a book. The latter is still sold, an advertisement stating that it "proves, by a rich array of facts taken from the life of animals and the evolution of human society, that

progress, biological and social, is best fostered, not by brute force or cunning, but by the practice of mutual co-operation and support." Romanes, the psychologist, found animals little less intelligent than man; Kropotkin, the sociologist, found them endowed with those virtues that make life in organized social groups possible and profitable.

The anecdotal method in animal psychology came to an end because it had brought ridicule upon itself by its endless flights into the realms of imagination, and because the experimental method promised results which, even if not interpreted alike by any two students, were yet capable of corroboration, since the conditions in which experiments are made can be controlled and adequately described. It was at this stage that animal psychology and animal sociology parted company. Experiments can be made upon isolated animals in a laboratory. The social lives of mammals cannot be studied in the same way. The result has been that information about mammalian social behaviour has continued to accumulate mainly in the form of travellers' tales—tales which seldom rest upon the accurate personal observation of their narrators; anecdotes in which factual and interpretative elements are inextricably mingled.

There are, however, exceptions. It has always been necessary for farmers and trappers to know something about the life histories of those mammals that are of economic importance, either because of the damage they do to land and crops, or because of the worth of their fur. When their value became a matter of national economy, systematic investigations of the specific zoological status, geographical distribution and life cycles of these mammals had to be made. It is difficult to say exactly when such studies were first begun. The earliest publication of the Biological Survey of the U.S. Department of Agriculture appeared in 1889,[256] but some careful studies had been written and published before that date. Unfortunately, how-

ever, even though the methods of these zoological surveys are a decided advance on previous studies in mammalian sociology, up to the present insufficient attention has been paid to the life cycles of the mammals concerned. Nevertheless, the accuracy demanded of these ecological studies by their economic importance set a standard which has stimulated further work in other fields of mammalian sociology. By 1919 the volume of such work had grown sufficiently to justify the appearance of the first number of the *American Journal of Mammalogy*. The recent series of investigations from the Oxford School of Zoology and Comparative Anatomy represent the first important mammalian surveys undertaken in this country.[31, 257, 102]

Monkeys and apes are of economic importance. Large land reservations have recently been made for the protection of the gorilla in north-eastern Belgian Congo. Many species of monkey have always been hunted for their fur. In South Africa baboons were at one time officially declared vermin because of the damage they do to farm lands. The Government subsidized the cost of their destruction, and between 1925 and 1927 over £8,000 were spent in bounties in the Cape Province and Transvaal alone. But in spite of financial loss incurred by the depredations of sub-human primates, it is only in very recent years that attempts have been made to obtain accurate information about their behaviour in the wild. As yet, moreover, no country in which monkeys occur has contributed towards such studies. The main body of information available to-day about the social lives of sub-human primates is still unfortunately anecdotal.

The behaviour of apes and monkeys has naturally attracted considerable attention in works on human sociology. In his *Principles of Sociology*, Herbert

Spencer summarized the information he had at his disposal about the social life of these animals.[332]

> "Among sundry of the *primates*, gregariousness is joined with some subordination, some combination, some display of the social sentiments. There is obedience to leaders; there is union of efforts; there are sentinels and signals; there is some idea of property; there is some exchange of services; there is adoption of orphans; and anxiety prompts the community at large to make efforts on behalf of endangered members."

These sentences, which Spencer calls "classes of truths", consist only of a series of interpretative generalizations based upon the anecdotal literature.

Because of the uncertainties involved in attempts to reconstruct a picture of primate social life from anecdotal accounts—the difficulties of separating the fanciful from the true, of assessing the value of stories whose origins are lost in the past, and of deciding between conflicting observations—sociologists have found it easy to convince themselves that the behaviour of apes supports whatever view they may happen to hold about the origins of human society. The lack of any exact knowledge in this field is clearly shown by the conflicting accounts they have given.

In the first volume of his *History of Human Marriage*, Westermarck discusses the origins of the "primeval habit" out of which developed the "institution of marriage". Numerous examples of family relationships are found to exist amongst animals, and an account, culled from many sources, of exemplary family life among the apes and monkeys is given. The gorilla "lives in family groups, consisting of one adult male . . ., one or more females, and one or more young ones of different ages, . . . the adult male, or father, guards, warns, and protects his family, and, apparently, builds a nest for them." "The family", the author continues, "implying marital and paternal care, was hardly less indispensable for primitive man than it is for the gorilla and chimpanzee."[377] Accord-

ingly Westermarck concludes that there is every reason to believe that primitive man lived in much the same way as his close relatives the apes. Alverdes[24] goes even further. He accepts a report that the gorilla is monogamous, and finds in this the "natural foundation" for the monogamy of human society. On the other hand, Briffault denies the existence of any permanent sexual relationship in the animal world. "The animal family, out of which the human social group must be supposed to have arisen, is matriarchal," and in proof of this statement he provides a rich array of relevant quotations from the anecdotal literature. He too emphasizes the behaviour of the gorilla, and cites some ten quotations to prove that whatever its mating relationship may be, it is certainly not monogamous, as one would gather from five of the six statements quoted by Westermarck. Briffault concludes that "male anthropoids are not in general permanently attached to a given group, but join a female, or group of females, as does the orang, according as their instincts prompt them". The females with their young form the true permanent group, and a female will admit a male only when she is "prepared for the exercise of his function".[53] According to Briffault, and also to Corin,[71] primitive human society was arranged on somewhat similar lines.

Stimulated by the conflicting accounts given by sociologists, Miller published in the *Journal of Mammalogy* for 1928 a paper entitled "Some Elements of Sexual Behaviour in Primates and their Possible Influence on the Beginnings of Human Social Development".[258] The paper was important not so much for its record of facts of primate behaviour, as for its insistence on the necessity for using only accurate data about sub-human primates in discussions on the origins of human society.

The particular work that drew Miller's criticism was Malinowski's *Sex and Repression in Savage Society*.[245] In this book Malinowski denied that any "type of

PLATE II

Photograph by J. E. Saunders

MEMBERS OF THE HAMADRYAS BABOON COLONY OF MONKEY HILL
in the London Zoological Gardens (See p. 218)

[*face p.* 14

human organization can be traced back to gregarious tendencies", stating that "the family is the only type of grouping which man takes over from the animal". In his development of the theme that the instincts which regulate family grouping among apes become transformed into cultural bonds in human society, he contrasted the sexual behaviour of the ape with the corresponding form of behaviour in human society. But he described the ape as having a generalized form of sexual behaviour, to which its known behaviour does not correspond.

In his discussion of the arguments of sociologists, Miller criticizes the view that man has a type of sexual psychology radically different from that of all other mammals. Malinowski described the ape as a creature with sharply defined periods of rut and heat. Miller cites evidence—in the form of quotations—to show that the female primate, unlike the female of almost any other mammal, is at all times ready to accept the male.

> "So far as they have been recorded in the laboratory," writes Miller, "the main features of simian sexual tendencies tally with well-known elements in human behavior; perhaps the only differences between the sexual life of man and that of other primates which can be reasonably considered as radical enough to have had any determining influence in shaping our peculiarly human institutions are these, that man appears to have developed two significant new features: a socially effective sentiment of love, and the physical and psychological possibility of rape. The first of these may, indeed, be less specifically human than the customary absence among laboratory primates of anything more than its most rudimentary features might cause it to appear. . . . That rape, on the contrary, is an exclusively human character seems to be beyond serious doubt."

Miller also denies that man has inherited from his primate precursors the tendency to live in family groups, maintaining, contrary to the views of most sociologists, that old world monkeys and apes live in loosely organized or sexually promiscuous bands.

The factual basis of Miller's statements will be

discussed in later chapters. They are referred to in this context, together with the views of Westermarck and Briffault, in order to indicate the confusion which at present faces those who wish to learn about the social lives of apes and monkeys.

The attention paid by sociologists to the behaviour of sub-human primates calls for an examination of the principles underlying comparisons between human and animal behaviour. This, in its turn, raises the further problem of defining the procedure for the development of a science of mammalian sociology.

CHAPTER II

MAMMALIAN SOCIOLOGY

THE similarity between anecdotal accounts of the habits of animals and ethnological accounts of the ways of primitive peoples makes it easy to understand why the two are so readily discussed together. Both are records of external forms of behaviour, records amplified in the case of man by introspective analysis and embroidered in the case of the animal with anthropomorphic interpretation. But although the ethnological approach is at present the only practicable way to knowledge of human social behaviour, the anecdotal method is already discredited in animal sociology, and has begun to give way before the methods of ecology and physiology. Apart from this, there are reasons which invalidate comparisons between the external forms of human and animal behaviour. Indeed, much could be said for divorcing the study of man's behaviour from that of other animals in relation to the subject matter of sociological discussion.

Many authors have maintained that human society differs fundamentally from any animal social grouping, and that any analogy drawn between the two is entirely false. If anthropomorphic interpretation is put aside, animals have only objective existence. None has articulate speech, none has any social institution. To the human observer their lives are a series of overt responses that are adapted to three main lines of behaviour—search for food, search for mates, avoidance of enemies. Up to a point these three ends limit an animal's activities in relation to its surroundings. Moreover, broadly speaking, behaviour along these lines is as direct as possible. For example, a monkey eats what it finds,

migrating or starving in lean periods; possesses what females it can hold; dominates or is dominated by its fellow creatures. All this can be discovered by observation alone. Theoretically, in any study of animal behaviour, the longer the period of observation is extended the more will be discovered, until eventually a point is reached when further knowledge can be obtained only by experiment.

The position is altogether different in the discussion of human social behaviour. Apart from external forms of response, one has to consider social institutions and articulate speech, which, as the records of history show, extend the variety of human behaviour so considerably that it becomes impossible even to attempt to determine its limits. No stretch of imagination would allow one to describe the social behaviour of even the most primitive savage in the same simple terms that are found adequate to describe that of the monkey. For man there is, in a sense, no state of nature. The human food gatherer, even though only a naked savage living in a rock shelter, reveals himself as a creature endowed with articulate speech and a moral code sustained by public tradition. He is often capable of undergoing a cultural transition of several thousand years by adapting himself to a complicated Western European mode of life—a life in which the three main lines of animal adaptive behaviour become masked. The range of human behaviour is so wide, the extent of human institutions so vast, that it is almost impossible to imagine the nature of the primary unconditioned stimuli and responses that in the child become harnessed and trained to the requirements of society.

In spite, however, of the immense gap between human and animal behaviour, it is important to recognize that the difference between the two is almost certainly one of degree only. Man's physical and mental kinship with other living organisms cannot be denied. But, as Briffault remarks,

"manifest as is the continuity between the human mind and the mind of animals, we have perhaps become too ready to rest satisfied with the fact that there is no unbridgeable gap between the two, and to underrate the character of the differences which they present. Not that any of those differences is unbridgeable, but, the transition being once effected, conditions have been set up which are radically different from those amid which the animal mind operates. Language and conceptual thought, and the consequent introduction of a separate hereditary transmission distinct from the physiological, constitute unprecedented conditions of evolution." [53]

Cultural phenomena may not, in the last resort, prove to be absolutely different from physiological events. But there is a significant distinction between the physiological responses of the animal and the cultural behaviour of man. The effective stimuli involved in the behaviour of animals are mainly inherent in immediate physical events, which are in no way the by-products of the activities of pre-existing animals of the same species. Man, on the other hand, amasses experience through speech, and the effective stimuli underlying human behaviour are largely products of the lives of pre-existing people. The environment within which human beings live is mainly the accumulation of the activities of previous generations. Culture, in this sense, is an essentially human phenomenon. It is conceivable that a clearer biological understanding of the nature of speech and its derivatives will eventually bring the materials of sociology within the scope of physiological interpretation. Meanwhile, however, a significant and convenient line of demarcation can be drawn between the respective fields of human and animal sociological inquiry.

The separation of man from the animal in discussions of social behaviour is valid only as a practical measure. A scientific philosophy, Hogben maintains,[179] does not allow of Cartesian compromise in the consideration of behaviour, and there can be no question that this point of view promises most in the long run for the advance

of knowledge. It is conceivable that the day may come when it will be possible to discuss adequately all forms of overt behaviour, human or animal, in the same terms. Behaviourist experiments may, in the future, reveal the nature of all human unlearned responses, and trace their growth as they are conditioned by the infinitely varied stimuli presented by a complex social environment. But since at present we lack this knowledge about our own behaviour, although we can, if we wish, provide ourselves with a fairly clear statement of the origin and development of animal social responses, it is vain to attempt as yet a common approach to the study of human and animal social behaviour. The differences involved, even though they be quantitative only, are too vast for such a project.

It is certainly unwise to take an opposite point of view and, regarding too optimistically the rapid progress of experimental psychology, to proceed in the discussion of sociology on the logical assumption that in the ultimate analysis of vital behaviour the responses of man will prove no different in kind from those of the earthworm. It is perhaps possible, as some maintain, that all external manifestations of behaviour will come within the scope of explanation of the conditioned reflex. If, as many experiments suggest, they do not, it is still probable that they will all come within the scope of explanation of some other concept equally well based upon phenomena that are established objectively. But to devise, as Alverdes has done, classificatory schemes of social behaviour to include both animals and man, on the assumption that all behaviour is fundamentally the same in kind, may be far more misleading than to conduct human sociological researches with implicit faith in the doctrine of man's separation from the rest of the animal world.

Alverdes is the author of the only modern work on animal sociology that has appeared in the English language.[24] He does not believe that the complexity and peculiar nature of human behaviour is in any way

an obstacle to discussing it together with that of other living organisms. He would explain all activity, whether human or animal, by means of a formula, $A = f$ (C, V), where A represents the act, C "the instinctive element in the actions of men and animals", and V the variable "which produces in some cases an appropriate, in others an unforseeable response to a situation". "Every act, A, is, therefore, at one and the same time a function of a constant, C, and a variable, V." "The difference between instinctive and intellectual activity is this, that in the former the constant, in the latter the variable predominates." Translated into terms of modern physiology, this formula simply means that all behaviour, animal and human, is built up of conditioned and unconditioned reflexes. A newly-born animal is capable of certain movements, which are built up of a series of reflexes, and which in the course of development become adapted to new stimuli and new situations. Alverdes' formula cannot mean any more, and because it means only that, it is, for reasons already indicated, hardly a sufficient basis for a system in which men, parrots, penguins and ducks are all classified together as illustrating the institution of permanent monogamy within a herd. It is true that birds mate because they have reproductive organs that periodically determine mating behaviour. It is equally true that the possession of reproductive organs is not unconnected with human marriages. In both we have what Alverdes would no doubt call the same "instinctive element". But the particular institution in which the mating impulse displays itself is determined, at any rate in man, by the "variable factor" of the act, "practice, experience, habit, also on occasion tradition". Whatever determines the alleged "permanent monogamy" of birds, it certainly belongs to a category different from those cultural factors responsible for human marriage. To classify both together in no way simplifies the problem of social behaviour. It only tends to mask the important fact

that animal behaviour is almost entirely on a physiological plane, while almost all human behaviour is conditioned by culture.

Whether or not the mating arrangements of the penguin, parrot and duck can justly be classified together is also doubtful. The three species may be permanently monogamous owing to entirely different physiological mechanisms. The common classificatory schemes that depend upon such superficial resemblances are all intrinsically anthropomorphic. From the point of view of scientific classification external forms have always to be looked upon with suspicion. Both bats and birds have wings. If wings were the criterion for classification, then the two would be grouped together. As, however, external form is usually disregarded in morphology, bats, as mammals with forelimbs adapted to life in the air, are completely separated from birds. If the principle of classification by external form leads to error in the sphere of morphology, it can do so even more in the sphere of behaviour. Animals differ profoundly from one another, in form, in physiology, and in the environment they inhabit. Social behaviour is the end product of the interaction of these different factors. Clearly, in the study of its behaviour, each animal must therefore be considered according to its own separate characteristics. The study of animal life will not be freed from anthropomorphic tendencies except by means of specialized research. Analogy, as Hogben has implied, will have to give way to analysis if there is to be an end to irrelevant and anthropomorphic classifications of animal society.

Apart, however, from the reasons suggested above, there is another that invalidates most comparisons of human and animal social behaviour. The behaviour of animals is referred to chiefly in questions concerning the origin of human institutions and human attitudes. Superficially there seems no reason why the principle of evolutionary succession, based upon physical relationships, should not be valid in theoretical analyses

of the development of human social behaviour. But, as is explained below, though this is a field in which comparison might prove useful, it is not legitimate to infer, as did Alverdes, that comparison of animal and human social life will enable us "to discover some of the basic instincts and impulses upon which the whole edifice of human society is reared". It is an unsafe assumption, born of anthropomorphic generalizations about animal behaviour and vague thought about evolution, that if human behaviour itself will not reveal those "basic instincts and impulses", comparison with the lives of other organisms will.

Human society takes the most varied forms. Few people find anything particularly remarkable in the fact that a handful of Bushmen, living in small food-gathering families in the Kalahari Desert of South Africa, exists contemporaneously with eight million civilized Londoners living crowded together in a few square miles. From the biological point of view, Bushmen and Londoners belong to the same species. No other mammalian species, so far as is known, shows such plasticity in social behaviour. When one is told that some wild rabbits live in burrows, there is usually no danger in supposing that all wild rabbits do the same. But similar suppositions are not always sound. Most writers describe the prairie dog of North America as an animal that lives in vast colonies. But according to the report issued by the U.S. Department of Agriculture, it is also found, especially in broken country, living in small family groups.[181] Since such variation in social life may occur within a single species of lower mammal, it is clearly unsafe to discuss external forms of behaviour in broad generalizations that embrace more than one species of a genus. The Lar gibbon, one of the lesser apes, is unanimously reported to live in small family parties, while the Hoolock gibbon is found only in large troops. If these reports are true, it follows that there can be no generalization about the social life of the genus *Hylobates*. Obviously, there-

fore, the very greatest care must be exercised before extending generalizations to include not only species and genera, but also families and orders. In practice this point is often overlooked.

It happens that the problems of human origins are largely and necessarily speculative. The data derived from ethnological studies seldom permit a unanimous conclusion regarding the ultimate sources of any particular custom. Such origins are lost for ever in that far-distant and mysterious past when Piltdown man, Pekin man, and the erect ape man of Java roamed over Europe and Asia. To-day no creature lives to bridge the gap between *Homo sapiens* and the anthropoid primates. The behaviour of the apes is therefore often made a basis for speculation concerning human origins. It is doubtful, however, whether the fact that the gorilla lives in family groups strengthens the view that the most primitive form of human society is—as Westermarck contends on the basis of existing records—the monogamous family unit of food-gathering peoples.* The fact that apes live in family groups is in itself no proof that the first men did the same. From the zoological point of view, man is not very closely related to the apes. In classifying the Order *Primates* it is customary to place them in different Families. Moreover, contrary to popular belief, there is no clear reason why the social behaviour of the "prehumans" should be considered to have been like that of apes rather than like that of monkeys. Most authorities maintain, on the basis of morphological resemblances, that man and the apes are related, and that both evolved from a common type after the monkeys had branched off from the main stem of the Order. Hence some systematists adopt the view recently given expression by Simpson [326] and combine the families *Hominidæ* and *Pongidæ* in one superfamily. Certain anatomists, on the other hand, associate man in his evolution with

* Disregarding the fact that similar analysis and similar argument have led other authors, for instance Briffault, to an opposite conclusion.

the gibbons, others with the monkeys, and at least one contemporary morphologist strenuously maintains that the human family separated from the main stem at its base, and that it evolved from tarsioid ancestors independently of the other primates.[384] These different views are founded on the same kind of evidence, and their authors all believe that man shows the greatest number of significant physical resemblances to the particular sub-human primate with whom they claim his closest kinship, explaining his resemblances to other primates as the results of parallel evolution. The time differences involved in these various hypotheses are—in geological terms—not extensive. They all imply that he began his distinctive human evolution at some period in the first half of the Tertiary geological epoch. Since geological time provides almost unlimited opportunities for parallel evolution in the primate order, there seems to be no logical reason for supposing that man's distinctive social behaviour evolved from any one group of primates rather than from any other.

The danger of arguing from the behaviour of one animal to that of another is, as already indicated, considerable. The spotted deer of India and the red deer of Western Asia belong to the same zoological family. The spotted deer breeds at all times of the year, a fact that implies continuous meeting of the sexes, while the red deer has a short mating season, the only time when the sexes meet.* If therefore it is impossible to generalize from the mating habits of the spotted deer to those of the red deer, it is even more misleading to attempt to infer the mating habits of the first men from those of the gorilla or any other sub-human primate, since they belong to different families. Furthermore, as Elliot Smith [98] has suggested, in spite of some significant resemblances there are other equally significant but inexplicable differences between the familial relationships of primitive food-gathering men

* Records of the Zoological Society [400]. Also Blanford,[46] Lydekker,[242] Sterndale.[336]

and those of apes. For this reason, and for the reasons explained above, it seems clear that discussions about the social behaviour of men now extinct, and known only by their fossilized bones, would still remain on the level of speculation even if everything possible were known about apes and monkeys.

It is not only in the sphere of social relationships that this argument holds. Kroeber in his discussion [222] of the "three principal approaches"—the archæological, the ontogenetic, and the comparative—to the question of the origin of culture, states that "comparison with those of the infra-human animals most likely to manifest anticipations of cultural activity" is difficult because of the paucity of established facts and the frequency of anthropomorphic misinterpretation. These may be the difficulties, but the comparative approach has the same shortcomings in discussions of the origin of culture as it has in those of the origin of human social institutions. Anthropologists may find intimations of the beginnings of culture in the facts that the chimpanzee lives in social groups, is possessed of acute powers of perception, and uses sticks as implements. They would find the same intimations in the behaviour of lower primates—both of the Old and of the New World, for recent investigations all tend to show the fundamental similarities in the social and individual responses of most sub-human primates.*

Thus only the behaviour common to all apes and monkeys can be regarded as representing a social level through which man once passed in the pre-human stages of his development. In the life of the monkey one may see a crude picture of the social level from which our earliest human ancestors emerged. But only that. The behaviour of the sub-human primate represents a pre-human social level, a level which, though without culture itself, seems to have contained the seeds that grew into the culture of primitive man.

* The term sub-human primate is used here to refer only to monkeys and apes.

PLATE III

Photograph by F. W. Bond

A NURSING BABOON AND HER BABY

The usual approach to the interpretation of the problems of the social behaviour of mammals is teleological, and involves a *petitio principii* by presupposing the existence of a specific "social instinct". Such a concept is perhaps necessary to interpret anecdotal and anthropomorphic accounts of animal life but, as Parr [284] remarks, it is "mostly used to veil a lack of knowledge of the real psychological or neurophysiological elements and reactions" underlying social behaviour. The teleological explanation of the origin of societies postulates that animals survive better in groups than as individuals, and the existence of animal groups is usually attributed to natural selection. It is perhaps conceivable that natural selection may have influenced the formation of group, as opposed to familial, life. If an impulse to live a herd life is a genetically determined response, one might assume, in the lack of any more obvious explanation, that animals living in large herds have survived because, possessing this inherited mechanism, they were able, as a herd, to withstand and conquer their enemies, whereas solitary animals were exterminated. But this is purely speculative, and the hypothesis does not suggest any method for its substantiation.

As Parr has shown, teleological speculation about "social instincts" can be disregarded in the explanation of such complex social behaviour as the milling of fish —the ceaseless swimming in circles of individuals within a school that as a whole remains stationary. According to this authority, there is a mutual attraction between individuals belonging to the same species of habitually schooling fishes; an isolated individual will react to its perception of a fellow by bending its course of swimming towards the source of perception. When it has approached, it ranges itself alongside its companion. The approaching response is regarded as a primary unconditioned reaction, and the adjusting of direction as a secondary or conditioned response. These two fundamental concepts explain most of the complicated forms of the social behaviour of fishes.

If teleological concepts are unnecessary for the consideration and interpretation of what might be regarded as obscure and non-adaptive behaviour in such low vertebrates as fish, they are even less necessary in the discussion of the more readily understood activities of mammals. When all questions of its applications to human behaviour are laid aside, and when teleological speculation is disregarded, the chief subject matter of a scientific mammalian sociology is seen to be ecology, reproductive physiology, and those influences which can be classed together as due to the variations of the individual.

An animal cannot survive outside the environment to which its physiology is adapted, while there is always a particular set of external conditions, such as temperature, humidity, and food supply, in which it can best live. Similar animals—individuals of a species—as a rule all live in one kind of environment because their needs are all much the same; and, apart from questions of fertility and disease, their numbers in a particular area will depend upon their ability to find adequate food and protection from enemies within its boundaries. Moreover, a single animal or a group of animals is attracted by an environment that includes its particular physiological needs, and repelled by one without them. The daily movements of the individual in search of food and protection, heat and shade, are probably, therefore, no different in kind from the migratory activities of vast herds of animals.

These ecological considerations show that environmental conditions are responsible both for limiting the size and for directing the movements of whole animal groups. Moreover, such external factors as temperature and food supply are also partly responsible for the immediate attitude of the individual within a group; and since either paucity of numbers or density of population may affect individual social responses, it is possible that external conditions may also indirectly influence social behaviour.

But social behaviour—the inter-relation of individuals within a group—is determined primarily by the mechanisms of reproductive physiology. Hitherto, this fact has seldom been accepted as a basis for discussion, most students having rejected it in favour of a teleological and anthropomorphic view of animal society. Among the few exceptions are Howard,[188] who has applied it in the study of bird behaviour, Malinowski,[245] who based upon it his argument about the differences between human and animal society, and Briffault,[53] who applies the view extensively in his discussion of a possible matriarchal foundation of human society. Briffault's opinion is very clearly stated. "The cause which gives rise to the formation of a group among animals, and the bond which holds such an animal group together, are in every instance manifestations of the reproductive instincts, and every association of individuals in the animal kingdom is, without exception, a reproductive organization." His application of this principle in sociological discussion is noteworthy, even though it is often reduced to doubtful generalizations based on anecdotal evidence. Apart from a few specialized researches to which reference will be made in a later chapter, no serious attempt has been made, so far as I am aware, to apply this view in the study of mammalian behaviour, as it has been applied in the study of bird behaviour. The life of almost any mammal will, however, show how nearly its social responses are a reflection of physiological mechanisms.

The Californian sea-lion (*Eumetopias stelleri*) has a breeding season that extends from June 15th to July 15th, and a gestation period of about eleven months. During the latter part of May, the cows band together, sometimes in the company of immature bulls, in the neighbourhood of the rookery where they will later meet the adult males. These arrive early in June, either singly or in groups of as many as six. By the middle of the month breeding activities are in full swing, and within

a week or so of giving birth, the cows come into heat and seek the bull. Bull sea-lions do not form harems in the same way as the fur seal, although some take up positions in the rookery which they endeavour to keep by fighting. As soon as every female has been served, the animals take to the sea and the sexes separate.[301]

The pattern of social behaviour exhibited by this species is clearly determined by its reproductive physiology. The sexes meet and engage in mating activity in only a small part of the year, because that is the only time when their reproductive organs are physiologically in a condition for mating. The fighting of the rutting males follows from their possession of physiologically active testes. The particular time that the females come into heat and seek the bull is determined by the fact that ovulation * follows soon after parturition. The separation of the two sexes at the end of the season is due to the transition of the reproductive organs of the male from a functional to an inactive or *anœstrous* state, and to the fact that the physiological condition of mating or *œstrus* in the female is replaced by that of pregnancy.

This example of the sea-lion illustrates how the framework of mammalian society is determined by physiological mechanisms. Reproductive physiology is the fundamental mechanism of society. Individual responses within a group are both limited by it and adapted to it, so that the most profitable classification of the societies of mammals involves the classification of their sexual mechanisms.

Social behaviour is compounded of the responses of all the individuals in a group, and the behaviour of the group will vary in accordance with the behaviour of its members. The greater the plasticity of behaviour of the individual, the greater will be that of the behaviour of the group. The responses of a monkey are much more varied than those of a ground-squirrel. Similarly,

* The shedding of ripe ova from the ovaries.

the behaviour of a group of monkeys is more varied than the behaviour of a group of squirrels. But plasticity in the individual and in the group is not determined by psychological factors alone. The mechanisms of reproduction may or may not be so fixed and sharply defined as to determine stereotyped forms of social response. Those of the monkey are less definite than those of the ground-squirrel, and this is directly correlated with its freer behaviour.

The argument outlined above goes far towards explaining the broad basis of sub-human primate society. The main factor that determines social grouping in sub-human primates is sexual attraction. Females attract males and males attract females. The limit to the number of females held by any single male is determined by his degree of dominance, which will again depend not only upon his own potency, but also upon his relationships with his fellow males. The occurrence of sexual individuals within a particular area will act as a stimulus to the expansion of the group, and the limits of expansion will be set both by the relationships within the group and by the environmental conditions within which the group lives.

These considerations form the basis of the subsequent discussion in this book. Lack of relevant information makes it impossible to discuss here the subject of the ecology of the primates. The following chapters are accordingly devoted to an account of the socio-sexual mechanisms of apes and monkeys, and a description of their society.

CHAPTER III

SEXUAL PERIODICITY

THE periodicity of growth and of reproductive life is more arresting than perhaps any other vital phenomenon. Nine months' intra-uterine gestation precedes a man's birth into the external world. Two years pass before he walks into a childhood that extends to puberty at fourteen, when his sexual organs first become active. In women reproductive life is divided into 28-day cycles, periods of pregnancy and nursing, and is curtailed by a menopause long before old age. In men it continues evenly and without interruption until they are overtaken by senility. The normal periodicity of all these phenomena is fixed within narrow and still inexplicable limits. There is no obvious reason why the human sexual cycle should take four weeks instead of six, and why gestation should last ten instead of five lunar months. At present there seems no more reason for the particular rhythm of these phenomena than there is for life itself. The rhythmical nature of physiological events is part of their make-up; the most that can be discovered by available methods about periodicity is the mechanism of its maintenance.

Sexual periodicity is even more conspicuous in the lower mammal than in man, since mating and breeding activity are often confined to demarcated seasons, instead of being diffused over the whole year. In such cases the quiescent reproductive organs of the male become physiologically active at fixed periods, and the reproductive organs of the female begin to undergo cycles of activity that are fundamentally the same as the 28-day cycles experienced by women. The essen-

tial characteristic of a mating season is that it recurs rhythmically at the same time of the year, irrespective of pregnancy and periods of nursing. Year after year, both male and female ferrets begin to be reproductively active in April, and at the end of August their generative organs shrivel up for the *anœstrus*, the annual period of sexual inactivity experienced by animals with mating seasons.[138] Among the larger mammals, however, it is possible that, though the male has an anœstrus, the female's reproductive organs may be continuously active, since her gestation is longer than that of a small mammal. Thus, in the sea-lion pregnancy lasts eleven months; in the remaining month of the year the animal may again conceive, since that is the season when its ovaries produce ova that can be fertilized by the semen of the male. Although such an animal does not have an anœstrus, it still experiences a definite cyclical mating season, which synchronizes with that of the other members of its species. Every year at this time rutting males impregnate those females that are experiencing their first season of reproductive activity, those that failed to become pregnant in the preceding season, and those that, having ended a period of gestation and nursing, have again come into heat. In some species gestation, by lasting longer than a year, may, together with the period of nursing, extend over two mating seasons. Even such species, however, will generate ripe ova and spermatazoa only at fixed times of the year.

As a general rule the male's period of reproductive activity is the counterpart of the female's. Thus the yearly season of sexuality in the male ferret roughly corresponds to that of its female. But the male season may sometimes begin earlier than that of the female, and there are also mammalian species in which the males remain reproductively potent throughout the year, even though their females experience breeding seasons and periods of complete anœstrus. For example, bitches have only two short sexual seasons a year, whereas dogs are always fertile. The reverse may also occur; the female

camel is said to experience a continuous series of reproductive cycles, and to be capable of conception throughout the year, while the male experiences only a short period of rut.*

Mating seasons are usually explained by the teleological principle that it is necessary for young to be born at a time of the year when climatic conditions are favourable and food is plentiful, and it is assumed that the time of the mating season is fixed, through natural selection, in accordance with this principle. On this view, the particular needs of the young of the species determine the time of the year when they are to be born, and the mating season precedes the time of birth by as many months as are required for gestation. Thus Marshall writes "the restriction of the breeding-habit to certain seasons may have been brought about under the influence of natural selection to meet the necessities of the offspring" [250]; while according to Westermarck this principle explains why "every month or season of the year is the pairing time of one or another species of Mammals".[377] Considered in a very general and broad way, this view provides an attractive explanation of mating seasons. It is conceivable that some animals were born with the capacity for giving birth at a particular time of the year, and that it was their young alone that survived to transmit the same trait, the offspring of the rest being eliminated by "natural selection".

This hypothesis is, however, sterile from the point of view of experimental analysis. Even as speculation it is based only upon a variable and intangible concept —the "necessities of the offspring". It is a common occurrence for different species of mammal living in the same locality to give birth at different times of the year. Teleological explanation would have it that this is due to the fact that the needs of the young differ from one another. Moreover, if mammals hap-

* Testimony of Major S. S. Flower. See also "*A Treatise on the One-Humped Camel*" by Captain A. S. Leese. Haynes. Lincolnshire.

pen to be born at times which we should anthropomorphically consider to be unfavourable, the fact would, on this view, have to be ascribed to a special need, not yet recognized, for being born at such seasons. The young of the American black bear, *Ursus americanus*, are born in the latter half of January, a most unfavourable time from an anthropomorphic point of view, for the mother is still sealed in her winter den.[315] Teleological explanation would imply that being born in January instead of in the spring or summer is a particular need of the bear, a need which, if unsatisfied, would threaten the survival of the species. Such a point of view clearly cannot help either the definition or the solution of the problems raised by the occurrence of mating seasons.

The platitude that almost all wild mammals have demarcated sexual seasons has seldom been examined critically. Based upon the fact that the more conspicuous mammals living in temperate zones have such seasons, this generalization has appeared in most works on the physiology of reproduction since the time of Aristotle. Thus in 1900 Heape[165] stated that with the exception of the primates, the reproductive systems of all mammals become inactive, in the absence of pregnancy, during a part of the year. The same author has asserted that even the primates ovulate and conceive only during short seasons, although their reproductive organs are never altogether inactive. The difficulty of obtaining accurate information relating to this question is great, and the few authenticated data about the breeding activities of wild mammals are scattered throughout an extensive literature. Many facts indicate that it is by no means true that all mammals have mating seasons, and it is significant that a relatively large number of the animals that have formed the subject of ecological investigations have been found to mate throughout the year. This applies to many small rodents, for example the field mouse, living in temperate zones.[31] Apparently, it is even

more true of tropical animals. Schuster [307] states that several mammals living near the mouth of the Rufigi in East Africa give birth at any time of the year, while Stevenson-Hamilton [337] gives records of dates on which pregnant specimens were obtained, which suggest that the lion has no demarcated breeding season. Unfortunately, data of this kind are too few to provide a basis for any generalization. Extensive records of the breeding of captive wild animals are contained in the histories of zoological gardens and menageries. There is, however, a common belief that such data are irrelevant to the question of natural breeding activity, since a captive life tends to disorganize reproductive mechanisms. Captivity may frequently result—as Darwin pointed out—in sterility. Whether or not it ever increases generative power is as yet unknown. Some authorities believe that it does, since domesticated mammals generally have extensive breeding seasons. But primitive man may have chosen his animals for this very reason. The belief that captivity may increase natural reproductive power is closely related to a view that, in a state of nature, the times and extent of breeding activity are directly controlled by environmental factors. If this view be correct, the records of breeding in captivity do not necessarily reflect the breeding activities of animals in the wild.

Heape, the chief exponent of the view that external conditions directly determine the extent and time of breeding activity, objected to the teleological theory discussed above, because there are some mammals whose mating seasons are separated from the time when they give birth by periods longer than are actually necessary for the intra-uterine development of the young. It is said, for instance, that in the bat the sperms introduced into the vagina do not fertilize an ovum until several months have passed, and that in the roe-deer the fertilized ovum remains quiescent in the segmentation stage for a considerable period. As an alternative hypothesis, Heape suggested that the

time of occurrence of the mating season is governed by climatic factors, and that the duration and recurrence of the season are influenced by variations in such external factors as temperature and food supply, and by "individual factors"—the peculiar morphological and physiological characteristics of a species—as well as by "maternal factors"—the length of gestation, lactation, and the period of recuperation following on these two phases. The hypothesis that the season of mating is determined by climatic factors is chiefly supported by such observations as suggest that the time of mating of a species differs "in accordance with the nature of the country in which it lives".[165] It is doubtful, however, whether this in itself implies that external conditions determine the time of occurrence of a breeding season. The facts of animal distribution do not in themselves necessarily provide evidence that different environments directly determine different breeding habits. It is probable that an animal inherits the fixed type of reproductive system of its species. Its particular sexual periodicity may be as much a genetically determined characteristic as is the shape of its head. Like the latter it may have appeared as a mutation or a series of mutations. Having appeared, natural selection determines whether the new character can survive in the environment in which it is produced. If it cannot, and if it is not transferred to some other set of external conditions by migration, it is eliminated. Unless, therefore, one assumes that in nature mutations occur as a result of environmental stimuli, the facts of animal distribution do not necessarily imply that external conditions have more than an indirect influence on the times of breeding seasons.

Heape's claim that the artificial conditions of domestication and captivity may, in some mammals, increase the duration and number of mating seasons does not appear to be well founded. Few of the relevant observations recorded by him in 1900 are conclusive. Many of his statements on the subject are qualified by

the word "probably". His conclusion that captive conditions prolong the mating seasons of wild mammals was reached by comparing his own uncertain records of their breeding habits in the wild with statements made by keepers in the London Zoological Gardens regarding the habits of the same animals in captivity. These statements were often incorrect. In any case, in the absence of *definite* knowledge about the breeding habits of most wild animals, the records of births in the London Zoological Gardens are no evidence for the view that captive conditions prolong mating seasons.

The few experiments bearing on the subject, that have been made under control and recorded, give little evidence that environmental factors, other than food supply, directly influence reproductive power.

There is certainly no evidence that abnormally low temperatures retard the onset of a mating season or in any way decrease the power of reproduction. Parkes and Brambell [282] failed to induce anœstrus in mice kept in cold-storage, and Baker,[31] who investigated the breeding activities of wild mice, found that there is "no correlation between the severity of the winters and the amount of reproduction during them". The field mice in Bagley Wood near Oxford did not breed in the winter of 1925–26. The cessation of reproduction was less marked in the following winter, while breeding continued, with only a small break, throughout the winter of 1927–28. As Baker writes, this would be "easily understandable if each winter had been warmer than the one before; but this was not the case". He also states that no sexually active males were caught in February of 1926, whereas all males caught in March were fecund, even though March was actually colder than February.

Light too appears to be an unimportant factor in determining the onset or extent of reproductive activity. Hill and Parkes [170] exposed two anœstrous ferrets to ultra-violet irradiation, but found that this had no effect

on the animals' sexuality. The ferret, which may be considered to be a domesticated animal, has an anœstrus that lasts from late August until the end of March. In laboratories it is kept under unvarying conditions, yet its mating season remains fixed between April and August. As Hill and Parkes point out, it is difficult to imagine what "environmental changes take place during April in an artificially-heated animal house, not particularly accessible to direct sunlight", that may determine the onset of reproductive activity. Baker also considers this question, and, by contrasting the diurnal bank vole (*Evotomys glareolus*) with the nocturnal field mouse (*Apodemus sylvaticus*), comes to the conclusion that neither light nor periods of general activity can be factors controlling the breeding seasons of these two animals.*

An obvious external condition that does directly influence breeding activity is nutrition. Numerous experiments have shown that deficient diets leading to inanition cause cessation of reproductive activity in laboratory mammals, and observation has shown that starvation has a similar effect upon man. It is also well known among farmers that rich feeding stimulates the fertility of sheep by increasing the number of twin births, and it is said that the practice of flushing—feeding luxuriantly—just before the mating season is expected, tends to hasten its onset. Heape writes that "different methods of feeding may accelerate or retard the time of season for ewes".[163] However, he does not cite evidence proving that artificial rich feeding increases the duration or hastens the onset of the mating season of any particular breed of sheep beyond the limits of reproductive activity shown by all sheep. Some breeds are more fertile than others; some have short mating seasons; others, like the Australian merino, are said to experience, in the absence of preg-

* When this book was in the press Dr. Baker informed me that certain experiments at present being carried out in his laboratory suggest that light has an effect upon the reproductive activity of the field vole.

nancy, a continuous series of sexual cycles similar to the human cycle. Several breeds, as Heape has shown, maintain their distinctive sexual habit when transplanted from their original homes to new environments. None of these facts indicate that longer breeding seasons are a direct effect of artificial conditions. The hypothesis that captivity has prolonged the sexual season of the wild prototype of the domesticated sheep is also speculative, since the habits of the sheep's ancestors are unknown. Feeding experiments have not hitherto been made on mammals with clearly marked breeding seasons. However, it seems improbable that an increased quantity of food would prolong the breeding season of such animals as ferrets throughout the year. Their breeding season still lasts only about four months, although they have been domesticated for countless generations.

That breeding activity is relatively independent of external conditions is seen more clearly when the habits of closely allied animals are contrasted. The bushbuck (*Tragelaphus roualigeni*) and the reedbuck (*Redunca redunca bohor*) live in the same area, eat the same food, and are exposed to the same climatic conditions; yet they differ considerably in their breeding habits. According to Schuster, the reedbuck breeds throughout the year, the bushbuck only in a limited season. The grey seal (*Halichœrus grypus*) and the common seal (*Phoca vitulina*) have similar habits and the same distribution. Yet the grey seal gives birth in February and the common seal in June.[241] Franklin's ground-squirrel (*Citellus franklini*) and the yellow ground-squirrel (*Citellus richardsoni*) live under much the same conditions in the same area. Yet the yellow squirrel regularly comes up after hibernation in the middle of April, whatever the weather, and then starts mating, whereas the Franklin's ground-squirrel does not emerge until three weeks later.[315] These differences are inexplicable on the view that the time of the mating season is directly determined by external conditions.

PLATE IV

Photograph by J E Saunders

A BACHELOR OF MONKEY HILL

(See p 248)

The observations recorded in the preceding paragraph suggest that much could be learnt about the effects of external conditions by examining the breeding behaviour of mammals naturalized in a climate completely different from that of their original home. Little, however, is recorded about the results of such transplantation. But Thomson,[353] in his book on the naturalization of animals in New Zealand, records a significant observation bearing on this question. One of his correspondents wrote, concerning wild goats, "the female has her young in winter, when food is not plentiful," adding, "why this is I never could understand." If true, this fact seems to suggest that the new environment has not altered the goat's European breeding habit. The reproductive seasons of many species of mammal that have been exhibited in the London Zoological Gardens practically without interruption for the past hundred years, do not appear to have been affected by the changed environmental conditions to which the animals have been exposed. Thus polar bears have been born in the London Gardens during November and early December, reindeer during May. Many other mammals from widely separated parts of the world show similarly restricted breeding seasons, some of which hardly seem to be adapted to the climate of London. Comparison with statements recorded in books of natural history suggest that most of these animals retain their original breeding habits.

The facts set out above seem to conflict with the widely held view that external conditions always play an important part in directly determining the time or extent of mating seasons and, indeed, they seem to indicate that the breeding behaviour of a species is part of its physiological constitution. An animal is either capable of giving birth at any time of the year, like the field mouse, or it does so during a restricted breeding season, like the ferret. Factors inherent in themselves, and not immediate external conditions, determine whether mammals have *absolutely* restricted breeding

seasons, or whether they are capable of reproduction throughout the year. This implies that records of the births of mammals in captivity do provide, contrary to common belief, a good indication of the breeding habits of wild mammals.

An important statistical consideration is involved in the interpretation of data regarding the breeding of captive mammals. Animals that are grouped under the same specific name in zoological gardens may have been collected in all parts of the geographical range of the species. Thus in considering the time of breeding of a species in captivity, comparison has to be made with the longest temporal span of the breeding power of the same species in the wild.

Owing to the lack of data, the problem of defining the natural limits of the breeding season of a wild species presents certain difficulties. Clearly the reproductive behaviour of a species is not that of a small sample inhabiting an insignificant part of the total area over which all the species is distributed. The individuals of such a sample might begin their breeding activities earlier in the year than those of a group living elsewhere. The first essential for a definition of a breeding season is therefore that it should cover the entire period in which all members of the species show sexual activity. It is conceivable that the sexual activity of individuals at opposite ends of the time range in any one year might not overlap. The definition must also take into account the behaviour of the species over a period of time in which it will have demonstrated its entire temporal range of breeding power. The necessity for making this provision is indicated by Baker's findings with regard to the field mouse, which reproduces to a different extent from year to year. An animal's mating season might begin in May one year, in April the next, and in June the one following. If the modal length of the mating season over a number of years is three months, the total range of the animal's mating activity would extend in the three years considered

over a period of five months—April to August. This period, and not the particular three months in which it mates in most years, represents the natural limits of its mating season. Further experience would tell whether or not the limits for the three years would prove to be the same as those for ten years.

Such a definition shows that it may not be necessary to assume that new environmental factors have unnaturally extended the reproductive power of individual captive animals when the breeding season of their species appears to be prolonged under changed conditions; for it is possible that the breeding habits of several varieties, distinct from the point of view of reproductive power, are included in the same designation in the estimation of the breeding seasons of species in captivity. At the same time it is also possible that captivity offers the necessary conditions to some species for an optimum expression of their generative capacities, —such, for example, as the natural conditions under which the field mouse, *Apodemus sylvaticus*, bred throughout the year instead of for six months.

The records of the Zoological Society of London extend without a break from 1827 to the present day.[400] Since the foundation of the Gardens, 745 mammalian species—excluding the Order *Marsupialia* and the Old and New World monkeys—have been exhibited.[111] Many of these species—which have been classified according to the methods of the museum systematist —would probably fail to satisfy the Linnæan demand that an animal should not be effectively fertile except with one of its kind. Of the 745 species, 251—a little more than a third—have bred. Since many accidental factors may be responsible for the fact that two-thirds have failed to breed, these figures do not necessarily imply that captive conditions usually cause sterility. Solitary animals may have been shown. Specimens may have died before reaching reproductive maturity. Organic disease of some other system may have affected the gonads secondarily. When animals

have bred, they have done so in natural circumstances. There is no record of any attempt having been made in the London Gardens to make animals mate under experimental conditions. Conclusions regarding breeding seasons can be based on the birth records of only 95 of the 251 species that have bred. For the rest, the records are too few to justify any generalization. Fewer births are necessary to show that an animal mates at all times of the year than to prove that it has a restricted breeding season. Thus it is fairly safe to assume that an animal has no breeding season if a small number of records are spread over the whole year. On the other hand, it is unsafe to assume that it has a mating season if a small number of births are crowded into a single month, since further records might show that the animal can breed at other times. The statistical value of all the data is greatly increased by the fact that they are scattered over a large number of years. Analysis of the data available for the 95 species that have bred sufficiently to allow of generalization shows that 8 of 15 species of the Order *Carnivora*, 5 of 21 species of the Order *Rodentia*, 3 of 3 species of the Order *Perissodactyla* (horses, etc.), and 24 of 48 species of the Order *Artiodactyla* (cattle, deer, etc.), have demarcated breeding seasons. In all, 47—one less than half—of the 95 species have breeding seasons, the remaining 48 breeding at any time of the year. This fact clearly suggests the unreliability of the statement that all mammals in a state of nature have restricted mating seasons. However, it must be emphasized that this method of analysis tends to swell the relative number of those species that breed at any time, not only because in their case fewer births are necessary to justify a conclusion, but also because mammals with unrestricted reproductive power are probably more likely to breed in captivity than are animals with demarcated mating seasons.

Knowledge of the breeding habits of wild monkeys and apes is as scanty as that regarding the lower mam-

mals. A view commonly expressed is that female monkeys and apes, though they experience a continuous series of menstrual cycles in the absence of pregnancy, are nevertheless incapable of breeding except during special seasons of the year. According to this view they are, therefore, like the greater number of lower mammals, whose breeding habits are known, in their restricted fertility, but differ from them in not experiencing a yearly period of anœstrus. This view of the reproductive habits of primates is based mainly upon the narratives of travellers, and these in their turn usually depend upon the testimony of natives. The following quotations indicate clearly the inadequacy of such evidence.

Winwood Reade,[290] who obtained all his information from native hunters, states that the male gorilla experiences a rutting season. Burton,[60] who also obtained his information from natives, maintains that the gorilla breeds about December, while Dyce Sharpe[316] observes that gorilla young are most commonly seen about February and March, the season after the early rains. Yerkes and Yerkes[395] quote a statement made by Wilbert, of the African station of the Pasteur Institute, that the chimpanzee "mates during the rainy season, August to October, and gives birth to young more especially from June to September. Sexual intercourse may occur throughout the year, and births are not strictly limited to any one season." Westermarck[377] quotes Möhnike in support of the view that the orang-utan experiences a sexual season, and states that Wallace told him (Westermarck) that he "found the young sucking orang-utan in May; that was about the second or third month of the dry season, in which fruits began to be plentiful." Huxley[193] writes, on the authority of Müller and Schlegel, that the old male orang, "except in the pairing time", lives alone. On the other hand, Hitzheimer and Heck[176] hold an entirely different view about apes (and monkeys), maintaining that they breed throughout the year.

According to Tickell,[355] whose knowledge of the Malay Peninsula was very extensive, the young of gibbons "are born generally in the early part of the cold weather. . . . The young one sticks to its mother's body for about seven months." Tickell does not indicate whether or not this statement is based on personal observation.

Heape[159] has given rather inconclusive records of the breeding habits of the Entellus langur of India, *Pithecus entellus*. In 1892 animal collectors sent him one hundred and eight specimens of *Pithecus entellus*. Of these

> "a considerable number had already borne young, and were suckling them; six were found to have very lately borne young, and one to be undergoing the process of aborting an advanced embryo; the rest were not breeding, and about fifty of these, adult females, were killed. . . . I was informed by the dealer —a Eurasian—who supplied me with these animals, that *S. entellus* breeds twice a year, in April and October, and that, when breeding, they retire into the thickest parts of the jungle, and cannot then be caught."
>
> "This information was doubtless obtained from native collectors, and all evidence supplied by natives was found to be so untrustworthy that little reliance can be placed upon this report.
>
> "Bearing in mind the fact that the animals examined were either not breeding, or else had recently borne young, it would seem fair to assume that there are one or more limited breeding-seasons for *S. entellus*, but my information warrants no further assumption."

Whether it warrants any assumption is questionable, but it certainly provides no evidence for the view Heape expressed in 1900[165]—"*Seminopithecus entellus*, from the jungles on the south bank of Hugli, has a definite time for reproduction."

Blanford[46] writes that the Himalayan langur has a breeding season, but does not state whether or not this opinion was based on his own observation.

Little is known of the genus *Cercopithecus*. Fitz-

simons[107] states that the Vervet monkey of South Africa, *Cercopithecus pygerythrus*, breeds in December and January.

There are several statements regarding the genus *Macaca*, that of Heape[161] being by far the most important. "Not less than four-fifths" of several hundred Rhesus macaques of India (*Macaca mulatta* = *Macacus rhesus*) sent him alive in February and March of 1891 "bore advanced embryos *in utero*, or had lately borne young, or had recently aborted the embryo". Most of the remainder—the number is not given—had not reached puberty, and, after excluding other "doubtful cases", he was left with seventeen non-pregnant females. Heape interpreted this evidence to mean that the Rhesus monkey has one or more definite breeding seasons, and because of a report that the animal reproduces at any time of the year in the Calcutta Gardens, he was led to believe that the species bred "at different times in different parts of the continent".

It is very doubtful whether this conclusion is justified. Heape's account unfortunately precludes definite estimation of the proportion of females in his collection that were actually pregnant or lactating. Very little is said of the sizes of the fœtuses, although he mentions that in two specimens he found "embryos of a stage probably similar to a six weeks' old human embryo", while the rest were "nearly full-grown". Nothing is said of the probable ages of those that had already been born, or of the conditions of the ovaries and uteri of those that had aborted their young. In fact, all stages of the menstrual cycle, of pregnancy, and of lactation may have been represented in his material. Further evidence is therefore necessary before the existence of a breeding season in wild Rhesus macaques can be accepted as proved.

On the basis of his own observations Hingston[173] concludes that the Himalayan Rhesus mates only once in a year, in September, the young being born in March.

Opinions differ about *Macaca irus* (= *Macacus cynomol-*

gus), the common macaque of the Malay States. Without giving the basis for his view, Ridley [295] writes that this species, even in confinement, breeds at only one period of the year. This too is the opinion of Van Herwerden,[365] who states that in the Island of Banka this monkey is fertile mainly in the period August–October. It is doubtful, however, whether Van Herwerden's anatomical evidence was sufficient basis for her conclusion. The material she studied consisted of ninety common macaque uteri that had been collected over a long period in the Island of Banka. Thirty of these were pregnant, and she based her conclusion about the breeding season on the fact that the sizes of the embryos in twenty indicated that conception had probably occurred some time between August and October. This conclusion was not supported by an analysis of the material indicating the proportion of pregnant uteri to all uteri collected in each month. Van Herwerden also published a graph showing clearly that *Tarsius spectrum*, a very primitive primate, breeds at all times of the year.

The data for this graph were compiled from the Utrecht collection of more than 1,000 uteri and ovaries of *Tarsius* collected for Hubrecht in the Island of Banka, and the curve was constructed from the absolute number of pregnant females taken each month. It shows that, though some were taken throughout the year, most of the pregnant uteri in the collection were taken in October and November, at the end of the dry season. Van Herwerden interpreted the curve as illustrating that *Tarsius* has an "inclination to a higher productivity in special œstrous cycles" [366]. But since it was constructed from absolute numbers, and not from percentages pregnant each month, it might also be interpreted as indicating that animal collectors are more active in Banka in dry and fine weather than in the rainy season. When the figures are arranged on a percentage basis, no significant seasonal variation in the birth-rate of this species is seen. This suggests

that the same error may have been made in the consideration of the data relating to the breeding of the common macaque. The possibility is supported by an observation of Blanford's, whose experience of the mammalian fauna of India and the Malay States was unrivalled, that in this species "there is no particular season for breeding".

According to Sclater[311] and "C.H.",[133] the young of the Gibraltar ape, *Macaca sylvana*, are born in spring and early summer. Living as it does in a state of semi-domestication, this species has been closely observed. Nevertheless, these reports cannot be accepted as final in the absence of details regarding the animal's ovarian and uterine cycles.

Little has been recorded about the genus *Papio*. Stevenson-Hamilton[337] writes, without giving the grounds for his opinion, that the young of *Papio porcarius*, the Chacma baboon, are born between November and February. Loveridge,[239A] however, states that the yellow baboon of East Africa, *Papio cynocephalus*, breeds throughout the year; this observer met with females carrying young in May, July and August, and shot a pregnant animal in April.

A few records have been omitted from this list of reports on the breeding of apes and monkeys, because they are even more vague than those quoted. Hardly any accounts are authenticated, and few provide other than anecdotal support for the generalization that apes and monkeys, although experiencing menstrual cycles throughout the year, nevertheless have restricted seasons of fertility.

Definite knowledge about the breeding of wild Old World primates exists, so far as I am aware, only in the case of the Chacma baboon, an animal that is widely scattered over South Africa. On the 4th of May, 1930, I succeeded in collecting on a farm near Grahamstown in the Eastern Province twelve adult females from one troop of baboons. Four of these were non-pregnant. Five were pregnant; one had an

embryo 2·5 mm. in length; another one of 16·5 mm.; the third one of 19 mm.; the fourth one of 65 mm.; and the fifth an apparently full term male fœtus with a crown-rump length of 230 mm. Three were lactating, and their babies were caught alive. One infant was estimated to be four months old, and the other two were each about two months.[398]

A complete reproductive cycle in the baboon—the shortest interval of time between two births by the same female—is approximately a year. A single menstrual cycle lasts one month, pregnancy lasts five to six months, and lactation, during which conception is impossible as ovulation does not occur, also lasts about six months. The females shot on May 4th were representative of practically all stages of the complete cycle. Some were non-pregnant. Some were in the early stages of pregnancy, and one contained a full-term fœtus. Others, again, were lactating, and one of these, judging by the age of her baby, would soon have restarted her normal menstrual cycles. This disparity between the different females proves conclusively that female Chacma baboons become pregnant at all times of the year in the neighbourhood of Grahamstown.

Pregnant females were not obtained elsewhere, but in many districts in which observations were made, nursing and œstrous females were seen together in the same troops. There is no evidence that reproductive conditions vary in different parts of the country, and it seems legitimate to conclude that one of the physiological characteristics of the Chacma baboon is that it breeds throughout the year.

The records of the breeding of monkeys in captivity indicate that in this respect the Chacma baboon is not peculiar amongst Old World primates. So far as it is possible to make generalizations, it can be stated that all Old World monkeys about which accurate information is available breed at any time.

Few accounts of the breeding of New World monkeys are available. Rengger[293] states that the howler

monkey, *Alouatta caraya*, breeds, as a rule, in June or July, and occasionally in May and August; the capuchin, *Cebus azarae*, in December; and the douroucouli, *Aotes trivirgatus*, between June and September. The same author, according to Forbes,[115] states that the young of the weeper capuchin, *Cebus apella*, are born in January. According to Rudolf Hermann and Spix and Martius (quoted from Hofschläger[178]), monkeys in the neighbourhood of the River Amazon breed in the last months of the year. Wislocki [380] has, however, shown by anatomical methods that the spider monkey, *Ateles geoffroyi*, the capuchin, *Cebus capucina*, and the howler monkey, *Alouatta palliata*, breed at all times. The same author tentatively suggests, on the basis of few data, that the squirrel monkey, *Saimiri ærstedii*, has a limited breeding season. On the other hand, as records of captivity show, the common marmoset, *Hapale jacchus*, breeds at any time[398].

Two conclusions of fundamental importance to mammalian sociology can be drawn at this point. One is that the greater number of lower mammals that have been investigated have a yearly season of anœstrus (cessation of sexual activity). The other is that monkeys and apes, like man, experience a smooth and uninterrupted sexual and reproductive life. The implications of these facts are discussed in the following chapter.

CHAPTER IV

THE BREEDING SEASON AND SOCIETY

THE distinction that is customarily drawn between "animal associations" and "animal societies" does not seem to depend upon more than a superficial analysis of the facts of animal behaviour. Accordingly there is reason to doubt the validity of the usually stated definitions of these types of social grouping. Alverdes[24] defines associations as "chance gatherings produced solely by external factors (e.g. insects round a source of light)". He considers societies to be "genuine communities which exist in virtue of some particular social instinct in the animals concerned (e.g. the ant state, a horde of monkeys). In short, no social instinct, no society!" Since the postulate of a "social instinct" implies ignorance of the factors underlying certain groupings, such definitions merely indicate that the stimuli drawing individuals together are better perceived in the case of "associations" than they are in the case of "societies". The distinction drawn by Alverdes, amongst others, between two types of animal grouping, though possibly not a natural one, seems nevertheless to have some empirical significance. It could be suggested that an animal association is a temporary union of individuals reacting in the same way to similar environmental stimuli, and that an animal society is a relatively permanent union of individuals held together by the mutual attraction of its members. Alternatively, the distinction might be defined by stating that an association endures only while a specified set of external stimuli are effective, and that a society persists in spite of great variation in external conditions. But as these definitions show, the repudiation of the concept of

specific "social instincts" does not facilitate the logical analysis of the facts of animal grouping. A line cannot be drawn between "temporary" and "relatively permanent". An association might continue through two different but succeeding sets of external conditions. External stimuli may include living organisms. For example, an animal, in making for a waterhole, might be drawn as much by its perception of other animals either at or journeying towards the water, as by its own appreciation of the pool. If the term "external stimuli" be taken in the restricted sense to exclude other members of the herd, the statement that an "association" is the result of external stimuli presupposes a particular, and not necessarily correct, interpretation of mimetic responses. Imitative reactions cannot be readily separated from other forms of mutual response. Moreover, as the preliminary analysis of this problem in Chapter II indicates, it is impossible in the consideration of social behaviour to dissociate ecological factors from factors that can be grouped together as part of the reproductive or social physiology.

The analysis of mammalian social behaviour is complicated still further by the occurrence of cyclical periods of reproductive activity. A brief mating season union of individuals that live in solitude during the anœstrus might be considered to be either an association or a society. Since such a group is a homogeneous and firm social unit held together by the mutual attraction of its members, it would satisfy the necessary qualifications of society, though it might not survive any varying environmental circumstance. It might be transitory, only lasting during a very brief physiological state of rut. Clearly, however, the relative permanence of the group is irrelevant in the consideration of this problem, since it is impossible to differentiate from any physiological point of view between a brief and a lengthy state of sexual attraction—a mating "association" of short duration and a continuous mating

"society". As this is impossible, search for distinctions would lead back to the definitions of society and association given above, and these, as has been indicated, do not even logically suggest that the two types of grouping are mutually exclusive. If the search were carried still farther it could, in the present state of our knowledge, only lead back to concepts of "social instincts" and "mutual aid". It is preferable, however, to avoid such elusive abstractions in the study of biological problems. It would therefore seem that at present there is no place in the discussion of mammalian behaviour for classification that depends upon what is probably an anthropomorphic distinction between animal associations and animal societies. The alternative, as was suggested in Chapter II, is to classify unions of individuals according to the underlying physiological mechanisms responsible for the mutual attraction of their members. The implication of such classification is that there is no significant and basic difference between permanent breeding societies and mating associations of short duration, whatever their size. The fundamental physiological factors that hold together a vast breeding school of seals or a horde of monkeys are the same as those which operate when a pair of foxes come together for the mating season.

For the purpose of sociological analysis, mammals can be divided into three main groups, the first of which comprises the monkeys and apes (Order *Primates*). The members of the second group are those of the non-primate or lower mammals that have an anœstrus and a demarcated mating season. The remaining, and smaller number of lower mammals, may be classified in a third group. They resemble the primates in breeding throughout the year and in not experiencing anœstrous quiescence of sexual activity, but differ from them in some important physiological characters that find their expression in a distinctive kind of social behaviour, different from that of the primate. This difference will be defined at a later stage.

Photograph by J. E. Saunders

AN ADULT FEMALE HAMADRYAS BABOON GROOMING HER OVERLORD

(See p. 57)

Amongst monkeys and apes, with few exceptions,* females are never found alone in their natural habitat, always being accompanied by one or more adult males. The orang is one of the exceptions. Reports about the behaviour of this animal are few and indefinite, but they seem to indicate that the sexes may sometimes be found apart from each other. Reference will be made to this observation in a later chapter,† where it is discussed in greater detail than is necessary at this point. The factor underlying the permanent association of the sexes is their uninterrupted reproductive life.[397] The sexual stimulus, even when weak, will draw male and female together. There is no evidence that in the primate it is ever overcome by any other stimulus, as it may be in a lower mammal such as the rat, in which it is sometimes outweighed by the stimulus of food.[267, 362, 371] The sexual attractiveness of a female monkey is, however, not constant, but varies rhythmically during the different phases of her reproductive life. It is strongest, as observation shows, about the middle of a menstrual cycle, but although it decreases greatly at other times, it is never entirely absent.[397] Since the reproductive phases of different females do not synchronize, sexual attractiveness varies among the individuals within a group at a given time. Statistical analysis of breeding records of captive monkeys suggests that there may also be a seasonal variation affecting the sexuality of all the animals of a group. Hartman considers the seasonal variation in the birth-rate to be sufficiently marked to justify the description of a breeding season in monkeys, basing his opinion mainly upon observations of his own colony of Rhesus macaques in the Carnegie Institute at Baltimore.[153] His animals conceived in almost every month of the year, but 28 of the 38 conceptions that occurred took place between October and January. Although he admits that they had less opportunity for copulation during summer, Hartman contends that this circumstance does not

* See p. 191 *re* capuchin. † See p. 179.

account for the variation in their birth-rate. He maintains that "the heat of summer is unfavorable to the monkey, at least *to the tropical monkey*," and that during this time "the sexes are far less interested in each other". He also holds that the females "do not conceive because they do not ovulate". Thirteen of fifty-nine laparotomies * which he performed were carried out during the "non-breeding season", June and July. All but one of the animals examined in this period had inactive ovaries, while only nine of the forty-six examined in the longer "breeding period" of the year showed a similar condition of reproductive quiescence. Hartman points out, however, that the proportion of the latter cases is actually much greater, since his figures tend to emphasize "the more favorable females in the more favorable times of the year".† Since this possibility exists, Hartman's explanation of the apparent summer sterility of his animals as being "due to the absence of an ovulatory cycle" does not appear to be conclusive. His observations have not yet received confirmation, and at present no other anatomical evidence is available to confirm his view of the existence of a seasonal period of ovarian inactivity either in the Rhesus or in any other monkey.

The only other monkey that is known to exhibit a seasonal birth-rate in captivity is the Hamadryas baboon (*Papio hamadryas*). A frequency curve constructed on the basis of 69 births that have occurred in the London and Giza (Cairo) Zoological Gardens shows that the greatest number of births have taken place between November and December, a fact that indicates an increased number of conceptions between April and August.[398] This conflicts with Hartman's statement that tropical monkeys are less active sexually during the summer months than at other times of the year.

* Direct inspection of the abdominal contents after incision through the belly wall. In his text Hartman refers to sixty operations. His charts indicate only fifty-nine.

† Hartman does not give any explanatory details of this fact.

But although records of births in captivity appear to give a fairly true picture of the breeding habits of animals, they may nevertheless be to some extent misleading. It is possible that a curve which shows an apparent increase of fertility between April and August in baboons confined in London and Lower Egypt may indicate little else than increased overt sexual activity in the better weather of spring and summer. It is conceivable that farther south, in the regions of their natural distribution, such variation would not occur. Moreover, since a monkey cannot as a rule reproduce more than once in a year, it is possible that a large number of fertile animals forming the basis of a breeding stock could establish a reproductive habit that might seem at first sight to be physiologically fixed, but which would actually be the effect of their regular breeding. It is still doubtful, therefore, whether or not a monkey shows true seasonal fluctuations in physiological reproductive activity.

The possibility that there is a seasonal variation in the birth-rate and sexual activity of the monkey does not affect the consideration of social structure, since there is no implication that the sexual stimulus holding individuals together is ever totally absent. Seasonal diminution of the reproductive activity of all the animals in a group would not disturb its intrinsic sexual basis, because a society would naturally hold together as long as its members were to any extent sexually potent.

"Flea-catching," writes Watson,[373] "regardless of what the sociologists may have to say, is the most fundamental and basal form of social intercourse between Rhesus monkeys." Monkeys, and to a lesser extent apes, spend a great part of the day grooming one another. An animal will carefully examine a fellow's coat with its fingers, eating many of the odds and ends that it finds. These are carried to its mouth either by hand or sometimes, after licking a tuft of hair, by direct nibbling. The performance implies exceedingly

well co-ordinated movements of the fingers, associated with exact accommodation and convergence of the eyes. This behaviour is commonly misinterpreted as an attempt to remove lice. Actually vermin are rarely found either on captive or wild monkeys. The fruits of the search generally turn out to be small, loose, scaly fragments of skin, particles of skin secretion, thorns, and other foreign matter. When not engaged in other pursuits, monkeys react immediately to the presence of fur by "picking". As is explained in a later chapter, the stimulus of hair is one to which a monkey responds as soon as it is born, and one which remains powerfully effective in all phases of its growth. In the lack of a companion a healthy monkey will pick through its own fur. Two, and sometimes even three, monkeys may, as a group, pick over one of their fellows. Usually the one being cleaned is passive, except for movements that facilitate the investigations carried out by its grooms. Sometimes, however, it may simultaneously be engaged in picking through the coat of yet another animal. Monkeys do not confine their grooming activities to their own kind. Any hairy object, animate or inanimate, may form the subject of their investigations. They readily pick over the hair of a human "friend". They may be seen in captivity, and have been seen in the wild, picking through the fur of animals belonging to different orders.[107] The performance seems to have sexual significance, not only because of its gentle stimulation of numerous cutaneous end organs, but also because it is sometimes accompanied by direct sexual activity. For this reason and because of its frequent expression, it is perhaps legitimate to regard the picking reaction and the stimulus of hair as factors involved in the maintenance of a social group of sub-human primates.

The second group of mammals that has been defined, includes those species that experience anœstrus and demarcated breeding seasons. The behaviour of many species belonging to this category bears out the view

that a social group endures as long as its members are sexually potent. When the reproductive organs begin to be physiologically active at the beginning of a mating season, the sexes seek each other's company. As soon as the mating season ends, and the reproductive organs (except in the case of pregnant or nursing females), resume their inactive anœstrous or non-mating condition, the sexual bond is broken, and the males and females part company.

The anœstrus is a convenient starting point for discussion of the social behaviour of this group of mammals. At least four sub-groups characterized by different modes of anœstrous life may be recognized.

The animals of the first sub-group are those that spend the anœstrus in solitude. During this period they are seldom found in pairs or in groups of more than two. Examples are the jaguar of Central America and the pocket gopher of the United States.

The second sub-group is composed of those animals, for instance the seal, that spend the anœstrus in separate male and female herds. The female herd includes the sexually immature young, while the male herd often includes the adolescent males. There is no clear distinction between this group of mammals and the first or solitary group, for often, as in the case of wild pigs, either males or females, or both, may wander alone or in small groups.

The third sub-group is formed by those species in which the sexes live together during the anœstrus without the sex differences having any social significance. Typical members of this class are the porcupine and the rabbit. Struthers'[348] statement that the Canadian tree-porcupine lives in this manner receives corroboration from the fact that keepers in zoological gardens are generally unable to distinguish male from female porcupines by their behaviour. The fact that sex differences have no social significance does not necessarily imply that sexual distinctions cannot be recognized in these mammals during the anœstrus. An

average buck rabbit is more powerful than an average doe both in and out of the anœstrus, and it is conceivable that at all times he is, in consequence, able to obtain more from a common food supply than his female fellows. But he does not derive any social advantage on account of his sexuality as such. Indeed, a buck rabbit during the anœstrus is merely the equivalent of a well-built eunuch. His bigger size is part of the complex of secondary sexual characters previously determined by the activity of the internal secretions of his gonads.

The fourth sub-group consists of mammals that are said to continue to associate in families* for some time after the mating season has ended. The wild horse, guanaco and prongbuck may be taken as representative of this class. The association in families does not as a rule continue throughout the anœstrus. The prongbuck of Northern America mates in late September. Before their testes are fully functional the bucks join small bands of nursing females that have collected somewhat earlier. When the rut sets in, the males fight and gather as many females as possible into harems, which then move independently but in fairly close territorial association with one another. As the females become pregnant and the mating season draws to a close, families once again unite to form herds of pregnant females, bucks, adolescent and young animals. In some areas in which it is found, the prongbuck does not migrate, and in others herds are formed only when the animals have collected in the districts in which they spend the winter. At the end of the cold weather, the herds—which in the years before the spread of civilization contained thousands of individuals—split up and the animals reappear in their summer range. The bucks wander in solitude or join to form small groups, and the pregnant females separate from each other as the time of birth (May–June) draws near. Finally, when

* The term "family" is used here to denote a male together with his harem and young.

their young are able to follow, the mothers unite to form small pre-mating season bands.[315, 130, 271] The general scheme of this yearly life cycle is a fairly common one amongst mammals, and it is sometimes suggested that the mating season groups endure as families even in the anœstrus. There is at present no evidence to support this view, and until such evidence is forthcoming there seems to be no reason to suppose that the post-mating season associations of such animals as the prongbuck differ in any fundamental way from those of the rabbit or porcupine. In the present state of our knowledge, it is impossible to define animal social relationships other than those of sexual male and female, and nursing female and offspring.

This analysis of anœstrous social relationships is both arbitrary and empirical. The behaviour outlined for each sub-group represents no more than an average type, and the four categories overlap considerably. An animal that herds during the anœstrus in one place, may elsewhere and at a different time roam in solitude. Lack of authenticated information makes it impossible to estimate the relative numbers of species belonging to each of the four categories, but an impression gained from fairly extensive reference to the available literature is that the sexes separate in the majority of species that have demarcated mating seasons.

If, as suggested above, all bisexual anœstrous associations are, in effect, asexual societies, the terms "permanent monogamy" and "permanent polygyny" cease to have any real meaning in the study of mammalian sociology. This is, of course, contrary to the view held by Alverdes, for he writes of many permanent relationships in which "the partners hold together either through several breeding periods or for the whole of their lives". He does not refer at all to mammals spending the anœstrus in herds in which there is no sexual discrimination. Nor does he cite any evidence, apart from a few references to anecdotal literature, in support of his views on the question. The only

method of proving that sexual relationships do extend from one mating season to the next would be to observe whether or not a rearrangement of mating groups occurs in each new mating season. Apparently no such observation has ever been recorded. Moreover, there is no evidence that any mammal prevents his fellow males from associating during the anœstrus with the females that were included in his mating season harem. Although Struthers' observations on the porcupine [348] indicate that anœstrous associations are asexual societies, they do not tell us whether or not a mateship may continue when interrupted by a long asexual interval. It is conceivable that it may. But even if it were to occur, there seems no reason to suppose that any male mammal is specially attracted year after year by the same female. The mating of the same individuals in successive years could be explained more readily in other ways. Almost all male mammals fight during the rutting season. The weaker animals are effectively eliminated, either by death or forced banishment, and the dominant individuals mate with the females. Fighting is as common in species which maintain an anœstrous bisexual association as in species in which the sexes separate. Indeed, it is striking that certain rodents and the guanaco—animals which Alverdes classifies as illustrating the institution of permanent mateships—are the very ones which, according to Darwin, "engage in desperate conflicts during the season of love".[78] It is conceivable that a particular male might remain dominant in a restricted area for more than one season. Even then it seems unlikely that he should succeed in deliberately collecting together in any one year the females with whom he mated in the preceding season. In the absence of data, therefore, it seems justifiable to regard permanent sexual relationships in periodically mating animals as being probably "accidental" occurrences not implying active selection. There are good reasons for considering that all relationships in mating

seasons pertain only to the seasons in which they occur. The idea of permanent sexual relationships conflicts with the annual transition of a sexual animal with functional reproductive organs, into an asexual animal with non-functioning reproductive organs. This seasonal alternation from sexual to completely asexual behaviour is outside the range of human experience. It is as if an animal were periodically castrated and then, after an interval, subjected to the operation of implanting a functional gonad.

Anœstrous herds are neutral herds. The females of these herds are in effect as much separated from males as they are in species the sexes of which separate immediately after the mating season. From the analytical point of view, therefore, the problem of anœstrous bisexual associations presents some aspects essentially the same as those presented by the anœstrous societies composed only of males or only of females. The first factor that helps to explain anœstrous unions is ecological. Animals of a species remain together in the same area because they respond similarly to the same environmental stimuli. As the instance of the prairie dog of Northern America shows, external factors play a big part in determining the size of animal associations.[181] Large bands may be formed in a suitable environment. Elsewhere the conditions may not allow of grouping. The more defined and limited the environment in which it can live, the more likely will a species be to form anœstrous associations. Speculative as they are, ecological considerations perhaps offer the best approach to the problems raised by the occurrence of anœstrous societies.

"Social" stimuli may conceivably also underlie anœstrous unions. It is possible that animals remain together because they are mutually stimulated by a herd smell. In conflict with this view, the special external scent glands possessed by most lower mammals appear in some cases to be active only during the mating season. Some lower mammals also engage in

mutual grooming activities. These are neither so well defined nor so frequently exhibited as the fur-picking activities of monkeys. It is conceivable that they help to hold together the members of anœstrous associations, though they are not superimposed upon a sexual background as they are in the case of the societies of monkeys. It might also be suggested that bisexual anœstrous association represents a form of social response conditioned originally by the mating season. That is to say, the sexually mature individuals under the influence of sexual activity acquire responses which, once acquired, become habitual. Teleologically this would imply that these societies are a means of keeping the sexes together for the next mating season. There are, however, more direct physiological mechanisms ensuring the meeting of the sexes.

When its reproductive organs quicken at the beginning of a breeding season, the character of the anœstrous mammal, and sometimes even its form, alters completely. The changes occurring in the larynx and scent glands are of particular interest. In the males of many species the larynx enlarges during every mating season, and as Darwin writes, "almost all male animals use their voices much more during the rutting season than at any other time," while others use them only at this time. This fact does not seem to have been the subject of experimental research as yet. It is possible that the effect of this seasonal physiological change is the attraction of the scattered members of a species. Many accounts in the naturalistic literature indicate that the call of one animal attracts another. Seasonal variations also occur in the external scent glands possessed by almost all mammals, with the exception of most monkeys and apes. These glands become especially active during the mating season. For example, according to Howell,[188A] the throat gland of the Californian mastiff bat is easily overlooked when inactive. During the mating season, however, it swells so as to become very obvious

externally, measuring 14 millimetres in diameter. In spite of a wide anatomical background, experimental analysis of the mechanisms of these organs has apparently not yet been attempted. Nothing certain is known about their functions, and several speculative theories have been suggested to explain their significance. One fairly common belief is that the pungent odours which the glands emit help to protect animals from the assaults of flies and mosquitoes. Another view is that they serve as weapons of defence, the assumption being made that their smell, usually obnoxious to man, is also obnoxious to other animals. Considering, however, the seasonal variations in the size and activity of these peculiar skin glands, it seems far more likely that they are related to reproductive behaviour. They are generally more prominent in the male than in the female. Darwin suggested that the odour of scent glands "probably serves to excite or allure the female", at the same time cautioning his readers that "we must not judge on this head by our own taste". He rejected the possibility that the scent gland odour serves to attract the female into the neighbourhood of the males on the strength of certain observations—given him by two of his correspondents—implying that the female mammal does not search for the male. As an alternative hypothesis he suggested that the presence of scent glands can be explained through sexual selection "if the most odoriferous males are the most successful in winning the females, and in leaving offspring to inherit their gradually perfected glands and odours".

It is unnecessary to discuss here speculative theories of sexual selection. The above mentioned observations which Darwin gave to explain his rejection of the theory that the glands serve to attract the females to the males are wholly inadequate. The naturalistic literature provides enough illustrations to indicate that females do seek the males. Moreover recent experimental work has proved that olfactory receptors are not

essential to immediate sexual behaviour in rats and guinea-pigs.* This fact may have wider application. It limits the possible field of activity of the scent glands, suggesting that their function is related either to the processes involved in the differentiation of the sexes or in the drawing together of the scattered members of a species, or to both. Scent glands, like the alteration in the voice, may still be regarded as mechanisms for bringing the sexes together.

Social mechanisms of this kind are almost unknown in the primates. Seasonal variations in the voices of monkeys or of apes have never been described; while cutaneous scent glands have been found only in marmosets, where they occur in the pudendal region,[381] in spider monkeys where two minute glands occur on the chest,[383] and in the orang,[383, 306] where a small external gland can be found, especially in the male, in the skin over the upper part of the chest. The gland in the orang diminishes in size very early in life, a fact suggesting that it is not a secondary sexual character. Nothing is known of the physiological properties of these glands, and nothing comparable occurs in other species of monkeys and apes. Some lemurs (a group of primitive and divergent primates) have modified skin glands, a characteristic perhaps correlated with the fact that they have restricted mating seasons.[400] The relative absence of these glands in monkeys and apes seems equally correlated with the fact that they live in permanently sexual societies.

Anœstrus does not interrupt the sexual activity of the lower mammals classified in the third sociological group defined earlier in this chapter. These species are fewer in number than those with demarcated mating seasons placed in the second group. The fact that they breed throughout the year implies that the sexes can always come into contact with each other. There are, however, no ready examples of big social groups

* See Chapter VIII.

PLATE VI

Photograph by J. L. Saunders

ONE BACHELOR HAMADRYAS BABOON GROOMING ANOTHER

(See p. 57)

Face p. 66

being formed by these lower mammals. The field mouse[31] and the reedbuck,[307] which belong to this third group, are usually found alone or in small parties. Although much has been written about the lion, it is still uncertain whether or not the females are always accompanied by mature males. The wood rat,[118] the lemming mouse,[59] and the deer mouse[305] are also usually found singly, though they are said to breed throughout the year. Even though the mammals belonging to this group do not seem to live in societies, it is obvious that the sexes cannot live widely apart from each other.

Although the mammals placed in this third group, like monkeys and apes, breed throughout the whole year, their social life differs from that of the primates in a very important respect. While they live mostly in solitude, the primate invariably lives in family or big social groups. This difference in overt social behaviour can be correlated with differences in reproductive mechanisms. The female primate is ready to accept the sexual advances of the male at all times, whereas the female lower mammal will mate, as a rule, only at those isolated intervals when she is in the physiological state of heat. This difference is discussed at greater length in the following chapters.

CHAPTER V

THE PHYSIOLOGY OF THE REPRODUCTIVE PROCESSES OF MAMMALS OTHER THAN PRIMATES

THE sexual responses of lower mammals are determined mainly by physiological changes the manifestations of which are gross enough to be plainly perceptible to human observation. The male lower mammal with functional gonads is in a physiological state that can be readily reflected into overt sexual behaviour, the appropriate stimulus for the full display of his mating reactions being a female in heat. His heterosexual responses will therefore be limited by factors operating in the females he encounters, and they in turn will seek his advances only while they are in the phase of desire—œstrus. The varied forms which associations of breeding individuals may take among the lower mammals are conditioned by the interaction of such physiological mechanisms.

The factors which determine masculine potency have been studied much less than the characteristics of the female reproductive cycle. The males of species that breed throughout the year are apparently always in the same physiological condition. Seasonal variations correlated with reproductive activity have not been described in any of their bodily systems, and their testes function without interruption. In this they differ conspicuously from mammals that mate during short periods of the year. These experience abrupt cyclical changes, the main one being the transition of the testes from an inactive to a functional state at the beginning of the mating season. This involves a great increase in the size of these organs and, in many species such as the

squirrel, their seasonal descent from the abdominal cavity to an external scrotum. The testicular change is accompanied in all species by a general increase in bodily vigour; in some by growth changes in the larynx; and in many by increased activity of the external scent glands. The correlation between the developmental phases of stags' antlers and periods of rutting is too well known to need description here.

Except at the beginning and end of the rutting season, the impulse to mate appears to be fairly evenly sustained and, judging from the naturalistic literature, every male tries to mate with as many females as possible. His success depends upon his vigour and dominance. Some animals do not feed during their mating season, and all become spent towards its close. The pugnacity of rutting animals is an expression of their physiological condition, and is not necessarily determined by the presence of females. It is exhibited at the appropriate season by animals confined alone in zoological gardens. Stags have been observed fighting during the mating season in the total absence of females, while bull seals fight each other not for females, but for territory in the rookery or mating ground. The facts provide little support for the usual anthropomorphic explanation that pugnacity in the mating season is immediately directed to the acquisition of females. Both the formation of harems and the maintenance of a particular position in a breeding ground can be regarded as forms of behaviour conditioned by the increased vigour of the rutting male. The fact that different females become receptive at different times is also possibly related to the formation of harems.

If growth changes are disregarded, the reproductive system is seen to be the only one in the body that does not maintain a constant anatomical appearance from the time of birth to the time of death. The cyclical changes that take place in the generative organs of the adult female mammal are much more elaborate than those that occur in the male.

As the anœstrus draws to a close, the blood supply of the ovaries and of the accessory reproductive organs—the uterus and vagina—is increased, and they grow in size. The physiological activity of the ovaries is shown chiefly by the cyclical development of follicles, which burst and discharge the ova they contain. *Corpora lutea*, organs of internal secretion, subsequently grow from the walls of the ruptured follicles. The ova are derived from the outer cellular covering of the ovary, the *germinal epithelium*, and each consists of a single cell which becomes covered by a layer of different cells called *follicular epithelium*. Such a system is called a follicle. In young follicles the ovum is directly covered by the follicular cells. In mature follicles it is separated from them by follicular fluid, in which it hangs suspended by a band of cells attached to the lining follicular cells of what has become a cyst. In the first stage of its growth the follicle makes its way from the surface into the substance of the ovary. The ovum itself reaches full size before the accumulation of follicular fluid separates it from the follicular cells. The follicle then expands, and the follicular or lining cells multiply in number, becoming several layers thick. As the *liquor folliculi* accumulates, the distended follicle approaches the periphery of the ovary, where in due course it ruptures and discharges the ovum it contains. After the ovum is extruded, the follicular cells are transformed into *luteal* cells of the secretory type, which multiply in number, and expand until the corpus luteum fills the entire shell of the follicle. In the event of conception, the period of growth of the corpus luteum is greatly extended, and it does not undergo retrogression until late in pregnancy. In an infertile cycle, the corpus luteum reaches its limit of growth in a shorter time, and degenerates sooner. The maturation of an ovum, its liberation, and the consequent development of the corpus luteum, represent a morphological cycle of the ovary.

A cycle of anatomical changes, running parallel to

the phases of the ovarian cycle, also occurs in the uterus, the shape of which varies greatly in different mammals. In almost all species except the primates it consists of two lateral tubes or "horns" usually united together by a single median tube, called the body. It is built up of two layers—a muscular layer, and a mucous membrane, or *endometrium*, which contains many glands. The uterine cycle consists essentially of endometrial growth during the ovarian phase of follicular growth, of endometrial degeneration at the time of ovulation, and of further and more conspicuous endometrial growth during the ovarian phase of development of the corpus luteum, a phase of growth which also ends with endometrial degeneration.

Rhythmical changes, correlated with these phases, take place simultaneously in the vagina. The vaginal wall consists of a muscular layer and an epithelial layer which has a characteristic appearance at different stages of the ovarian cycle. The vaginal cycle consists of a phase of epithelial growth, alternating with a phase of cellular death or *cornification*. The outermost cells of the vaginal epithelium lose their nuclei, and, becoming horny, are shed into the vaginal canal. The maximum amount of cornification occurs at the time of ovulation, after which the epithelial layer is invaded by white blood cells, or leucocytes, which, it is believed, help to clear away the degenerated epithelial cells. In most species these epithelial changes facilitate mating. They are so conspicuous that the chief method employed by the experimental biologist for determining the time of ovulation in laboratory mammals is examination of the vaginal cellular contents—a method that is now widely known as the "vaginal smear technique".

Cyclical phases of growth also occur in the mammary glands, which vary in number in different animals from a single pair to as many as nine pairs. During anœstrus, except for periods of nursing or pregnancy, the ducts of the glands are very small. During the mating season they undergo stages of growth that run

parallel with the phases of the ovarian and uterine cycles. The change is inconspicuous during the period of follicular growth. That occurring during the life of the corpus luteum is, on the other hand, considerable, and is responsible for transforming the mammary gland into a functional organ.

These separate morphological cycles are all part of what is called the *æstrous cycle*. They are grouped together under this designation because the most prominent symptom of reproductive periodicity is the "œstrus"—heat, frenzy, or passion—shown by the animal at the time of ovulation. Œstrus, marking the time when mature ova are discharged from the ovaries, divides the œstrous cycle into pre-ovulation (pro-œstrous, or follicular) and post-ovulation (or luteal) phases. The great alteration in the behaviour of the animal at the time of ovulation is directly correlated with the specific morphological changes that then occur in the accessory reproductive organs. Œstrus, which is the culminating event of the follicular phase, is usually the only time when the female of the lower mammals will mate. If conception occurs at the first "heat" of a mating season, the luteal phase that follows the fertile ovulation becomes the luteal phase of pregnancy. If, on the other hand, fertilization does not occur, it becomes a *pseudo-pregnant* phase. The corpora lutea are the agents determining changes that prepare the uterus for the embryo, and they also influence behaviour by stimulating maternal responses.

So far as is known, most mammals ovulate spontaneously, but at least two—the ferret and the rabbit—require the stimulus of copulation before the follicles in their ovaries rupture and the ova are freed to meet the semen. Some mammals, such as the bitch, experience only one œstrous cycle during a mating season, which, if infertile, is followed by anœstrus. Polyœstrous mammals, such as the rat, experience in the absence of pregnancy a recurrent series of œstrous cycles. Some polyœstrous animals have limited breed-

ing seasons, and others can give birth throughout the year.

The essential nature of the œstrous cycle is probably the same in all mammals, but its duration, and that of its constituent follicular and luteal phases, varies from species to species. The greatest relative variation occurs in the duration of the luteal phase, which obtains its fullest expression in the event of pregnancy. The pseudo-pregnant state is generally shorter than the pregnant, and varies in degree from animal to animal. In the unmated rat it passes unnoticed, œstrus recurring every five days, whereas in the marsupial and dog its duration is usually the same as that of true pregnancy. Sufficient morphological change may be occasioned to influence behaviour considerably. Many animals begin to build nests in preparation for non-existent young. The morphological changes in the reproductive organs are also by no means uniform in all the lower mammals. They vary considerably, and some knowledge of them is required for the proper interpretation of the œstrous and menstrual cycles. The changes that occur in the dog, the rat, the mouse, the rabbit and the ferret may be taken as representative of those found in all the lower mammals that have hitherto been investigated.

The reproductive processes of the bitch have been extensively studied. As was mentioned above, if it does not conceive during a mating season, it again passes into anœstrus. If, however, pregnancy occurs, lactation extends into what would have been the next anœstrus. The follicular phase lasts at least ten days, the pseudo-pregnant phase eight to nine weeks, pregnancy nine weeks, and the period of nursing continues for about an equal time. Conspicuous cyclical changes take place in the reproductive organs. During anœstrus the ovary does not contain either large follicles or corpora lutea, and the uterus is avascular and thin, its low mucous membrane containing few glands. At the beginning of the ovarian follicular phase, the

endometrium starts to thicken and the glands to secrete. At the end of this period ovulation occurs and degenerative changes take place in the uterine mucous membrane. The smaller capillaries break down and blood leaks out into the tissues of the mucosa. The superficial endometrial epithelium is also destroyed, blood escaping into the body of the uterus, and so to the exterior. As the corpora lutea develop in the shells of the ruptured follicles, the uterine mucosa regenerates, growing considerably even in the absence of pregnancy. About eight to nine weeks after ovulation, the mucosa once again breaks down, and simultaneously the mammary glands, which have also undergone a phase of pseudo-pregnant growth, secrete milk. When the phase of pseudo-pregnant degeneration has ended, the reproductive organs resume their anœstrous appearance.*

The mouse and rat are polyœstrous mammals that are usually capable under normal conditions of breeding at any time of the year. The length of cycle in the unmated mouse is five days—that is to say, ovulation and œstrus recur in that time if the animal fails to mate. The luteal phase is inconspicuous in these cycles and, normally, there is no pseudo-pregnant interval. Such a phase develops only after the stimulus of sterile mating and in that case œstrus, instead of recurring in five days, reappears in twelve. The delay is due to the occurrence of a seven-day pseudo-pregnant period, which is dependent upon the formation of functional corpora lutea. Gestation in the mouse lasts nineteen days. The animal ovulates within twenty-four hours after parturition, and corpora lutea develop in the discharged follicles. Lactation, during which œstrus does not normally recur, continues for three weeks, and the first ovulation to follow the post-partum œstrus marks its close. Since a mouse can be fertilized immediately after parturition, it can be pregnant and nursing at one and the same time.

* See Marshall.[250]

In both the rat and the mouse, as in the dog and other multiparous species, a number of large-sized follicles rupture at every œstrus. Corpora lutea develop during the two days following ovulation, and in the unmated normal animal reach their full size in about three days, degenerating before the œstrus that follows two days after their maximum development. No follicles develop during the pseudo-pregnant interval that follows sterile mating, nor does ovulation occur during true pregnancy or, after the post-partum ovulation, during the lactation interval of three weeks. The inhibition of follicular growth during these periods is usually ascribed to the functioning of the corpora lutea.

At the beginning of the follicular phase, the small and poorly vascularized uterus begins to enlarge, and by the time of ovulation it is about twice its normal diameter. This increase is due almost entirely to distension of the uterine lumen. According to Allen,[20] conspicuous degenerative changes, unaccompanied by reparative processes, occur in the lining epithelial cells at the time of œstrus. During the phase of pseudo-pregnancy that follows sterile mating, the endometrium grows extensively, and at the close of this interval of twelve days, when the corpora lutea of pseudo-pregnancy degenerate, hæmorrhage may occur into the body of the uterus.

Extensive studies have been made of the vaginal cycle in both the rat and the mouse, since the changes that occur are very pronounced. They follow the general plan outlined earlier in this chapter. At the beginning of the follicular phase the vaginal epithelium grows and becomes several layers thick. The cells that are thus formed subsequently degenerate and, becoming cornified, fall off into the lumen. This change occurs at the time of ovulation. Large numbers of leucocytes then invade the vaginal wall. The presence of cornified cells alone in a vaginal smear indicates that the animal is in œstrus.

The character of female reproductive activity in the

rabbit * and the ferret † presents a somewhat unusual feature, since these two animals only ovulate after the stimulus of mating. If mating does not occur, œstrus persists throughout the breeding season; whereas if it mates freely, the rabbit may have several litters. Both animals experience a pronounced pseudo-pregnant phase after sterile copulation. Mature follicles, which develop at the onset of the reproductive season, persist in the ovaries until mating occurs. If the animal does not mate, they degenerate (become *atretic*) at the approach of anœstrus. Ovulation in the rabbit usually takes place ten hours after copulation, and, if sterile, the corpora lutea continue to develop for only fourteen days. At the beginning of the mating season, growth occurs in the endometrium. Degeneration at the time of œstrus has been found only in the ferret. After ovulation the uterine glands experience a phase of rapid growth. It is believed that their secretion provides the initial nourishment for the embryo before implantation. The mammary glands undergo little growth during the follicular phase, and remain small until ovulation takes place and the corpora lutea become functional. Under the influence of the corpora lutea the glands experience a second and extensive period of growth.

The fundamental plan in all these types of œstrous cycle is always the same. During the follicular phase a certain amount of growth occurs in the uterine mucosa. The slightly hypertrophied endometrium subsequently degenerates at œstrus. Corpora lutea develop after ovulation, and the uterus simultaneously undergoes another phase of growth. In sterile cycles the period of pseudo-pregnancy usually ends with a second phase of uterine degeneration.

Three main problems arise in the discussion of the physiological mechanisms underlying these morphological changes. The first concerns the changes occurring

* See Parkes [281] and Hammond and Marshall.[137]

† Hammond and Marshall.[138]

during the follicular phase, the second those of the luteal phase, and the third the regulation of ovarian periodicity.*

The synchronization of the growth cycles in the accessory reproductive organs—the uterus, vagina, and mammary glands—with the phases of ovarian activity suggests that the two are functionally inter-related. This inference has received ample experimental confirmation, and it has been proved that the cyclic changes in the accessory organs are determined by internal secretions of the ovary. If the ovaries of any mature mammal are experimentally removed (the operation of *ovariectomy*), all cyclic activity in the accessory reproductive organs ceases almost immediately and the organs slowly atrophy. If ovarian grafts are transplanted into an ovariectomized female, atrophy does not occur, and in favourable circumstances œstrous cycles may continue.

The extraction of physiologically active preparations from the ovary has shown that the morphological changes occurring during the follicular phase of the œstrous cycle are due to a hormone, or internal secretion, known as *æstrin*. Originally this substance was always referred to as the *follicular hormone*, on the assumption that it was mainly derived from the follicular fluid. Soon after its identification, however, it was found to be present not only in the ovaries, but also in the placenta and in the circulating blood. To-day the hormone is chiefly obtained by extraction from urine, in which it is excreted. The site of its origin still remains obscure.

The physiological properties of œstrin have been tested and demonstrated on ovariectomized animals whose accessory reproductive organs have atrophied. The injection of œstrin into such animals produces all the anatomical and physiological extra-ovarian symptoms of the normal œstrous period. In the

* These problems are discussed in detail by Parkes [281], who provides a full bibliography up to 1929. Relevant facts from the more recent literature are incorporated in the account given in the following pages.

ovariectomized rabbit, mouse, rat or guinea-pig, it leads to development of the vaginal epithelium and to cornification, as well as to the uterine changes typical of œstrus in each of these species. Injection of œstrin into the normal animal just before the expected onset of œstrus is followed by an exaggeration of the normal morphological features of œstrus, although the ovarian cycle remains unaffected. Indeed, if enough of the hormone is injected, œstrus can be produced at times when it would normally be in abeyance. It can be brought about during the anœstrus, during lactation, and during pregnancy. In the lower mammals œstrus thus produced usually results in abortion. Artificially induced œstrus does not, as a rule, lead to ovulation at periods when it would not otherwise occur.

Although usually the manifest signs of the secretion of œstrin are sharply confined to the follicular phase of the œstrous cycle, certain of its characteristic effects are on rare occasions exhibited during the luteal phase. Nelson [272] observed physiological œstrus (determined by the vaginal smear technique) during the pregnancy of an albino rat. From records of the muscular activity of the same species, Slonaker [328] inferred that though "typical œstrual rhythm" is absent during gestation and lactation, œstrus may sometimes occur on the fourteenth day of gestation. The mare is said to ovulate regularly during the luteal phase of pregnancy.[67]

No satisfactory explanation is as yet forthcoming for the abundance of œstrin in the placenta and body fluids of pregnant animals, nor is it understood why, though present in such amounts, it yet fails to produce either œstrus or abortion. It is clear, however, that it is in no way responsible for the morphological and physiological changes either of pregnancy, or of the pseudo-pregnant luteal phase. Experiment has proved that œstrin does not cause any of the post-ovulation changes that occur in the vagina, the uterus and mammary glands. Prolonged and continuous injection of œstrin will not produce extensive proliferation of the

PLATE VII

Photograph by J. E. Saunders

TWO OVERLORDS AFTER THE REMOVAL OF THEIR FEMALES FROM MONKEY HILL

mammary gland ducts, or do more than induce the condition of the uterine mucous membrane typical of the physiological period of ovulation or œstrus.

The changes of pseudo-pregnancy and pregnancy—those characteristic of the luteal phase—are due directly to the activity of secretions produced by the corpora lutea. Normally, the corpus luteum that develops in the unmated cycle of the rat does not become functional, but the twelve-day inhibition of œstrus following sterile copulation may be due to the development of effective corpora lutea. Experiment has shown that another important function of the corpora lutea is to sensitize the uterus so that the fertilized ova readily become embedded. In many animals the normal anatomical manifestation of uterine sensitivity is the great post-ovulatory development of the mucous membrane and its glands. Removal of the corpora lutea soon after ovulation inhibits the development of the changes typical of pseudo-pregnancy. The sensitivity of the endometrium during the luteal phase may be demonstrated by instrumentally irritating the uterine mucous membrane during a normal pseudo-pregnancy. This procedure is followed by the development of large masses of hypertrophied endometrium—*deciduomata*. If the corpora lutea are removed before this experiment is begun deciduomata are not produced. That the presence of corpora lutea is essential for the attachment of fertilized ova to the endometrium has also been proved by their experimental removal, and by the artificial stimulation of their growth. Experiment has also shown that the presence of corpora lutea is essential for the full development of the mammary glands. But however much growth is stimulated, neither unlimited administration of corpus luteum extracts nor implants of the tissue itself will induce milk secretion. The factor responsible for mammary secretion has been proved, both by Corner[74] and by Nelson and Pfiffner,[273] to be the secretion of the anterior lobe of the pituitary gland. Another function that is usually attributed to

the corpus luteum, on the grounds of experimental and observational data, is the maintenance of pregnancy. Mice that have had a single ovary sterilized or destroyed by means of X-rays readily become pregnant from the remaining normal ovary. If that ovary is removed during pregnancy, when it contains corpora lutea, abortion of the embryo follows in a very short time. Conflicting results have been obtained, however, in experiments on other animals.

The mechanisms underlying the maintenance of reproductive periodicity are obscure. Originally it was supposed that the ovaries themselves directed the œstrous cycle, and both the follicles and the corpora lutea have at one time or other been thought to be the significant agents regulating periodicity. The corpora lutea were considered to be the more important because their functioning undoubtedly delays the appearance of the next œstrus, and their removal, when in an active state, is closely followed by maturation of follicles. This theory was discarded because œstrus does not always succeed degeneration of corpora lutea, for instance during pregnancy. The ovarian follicles were thought to be significant because their periodic development and rupture not only directly determine the growth of corpora lutea, but also appear to be indirectly responsible for the cyclical changes in the accessory organs. This view was finally abandoned when it was shown that destruction of all the ovarian follicles of the mouse by X-ray irradiation in no way disturbs the periodicity of the œstrous cycle in the unmated mouse.*

Although the basis of reproductive periodicity has not yet been fully explained, experiment has proved conclusively that the anterior part of the pituitary gland, and not any reproductive organ, is responsible for its regulation. The control exercised by the anterior lobe of the pituitary gland on the reproductive

* These experiments on mice have been confirmed by other observers. Recently, however, Genther has shown that X-ray irradiation of guinea-pigs may stop the œstrous cycle.[124]

organs has been demonstrated in many ways. In the rat, surgical removal of the pituitary stops the œstrous cycle. Injections of extracts of the anterior lobe of the pituitary gland into the immature mouse result in the precocious appearance of the œstrous cycle, which may be accompanied by normal ovulation. Injection of large quantities of saline extracts of the gland stops the œstrous cycle of the adult animal by converting follicles into corpora lutea without the previous occurrence of ovulation. Cessation of injection, with the consequent degeneration of the corpora lutea, is followed after varying periods by the return of the cycle. The anterior lobe of the pituitary gland is also normally responsible for the occurrence of ovulation. The rabbit ovulates ten to fourteen hours after the stimulus of copulation. If the pituitary gland is removed no later than an hour after copulation, ovulation does not occur.[103] The animal will ovulate, however, if this experimental procedure is followed by injection of extracts of the anterior pituitary gland of the ox.[171] Ovulation can also be induced in intact œstrous rabbits, without the necessity of previous copulation, by the injection of anterior lobe extracts.[38] A similar result is obtained by the injection of anterior lobe extracts into the anœstrous ferret.[170] Follicles mature and ovulate without the normal stimulus of copulation, while typical œstrous changes are induced in the uterus, vagina and vulva. These effects of the pituitary gland are by no means confined to mammals. It has been shown that mature toads ovulate upon injection of anterior lobe extracts, and that the ovaries of these animals retrogress to the embryonic condition after complete removal of the gland.[180]

These experimental data suggest that the anterior lobe of the pituitary gland stimulates the reproductive organs into activity at the beginning of a mating season, and that it is responsible both for their maintenance in a functional state and for regulating the phases of their activity. Its removal leads to atrophy of the repro-

ductive organs. Its injection into intact mature animals during anœstrus precipitates the onset of reproductive activity. It has a similar effect on immature animals. It seems to be responsible for the periodic occurrence of ovulation. The evidence indicates that in the rabbit and ferret the stimulus of copulation acts in some way, as yet unknown, upon the gland, which then, through its secretion, determines the rupture of mature follicles. During pseudo-pregnancy and pregnancy, it does not stimulate the ovaries to ovulate. It is conceivable that the corpus luteum reciprocally stimulates the gland, inhibiting the secretion of its œstrus- and ovulation-producing substance. Presumably, the anterior lobe is also responsible for the cyclical action of œstrin on the vagina and uterus, and by controlling the development of the corpus luteum it is indirectly responsible for the luteal changes in the accessory reproductive organs.

It does not seem that the pituitary gland influences the accessory reproductive organs entirely through the agency of the ovaries. By injection of extracts of the gland, Corner has induced milk secretion in the ovariectomized rabbit. In a similar way uterine degeneration has been obtained in ovariectomized monkeys.[155] Nevertheless, the influence of the pituitary gland upon the reproductive system seems to be mainly dependent upon the ovaries. When these are removed it cannot prevent the consequent atrophy of the accessory reproductive organs. Many problems concerning the pituitary gland still require elucidation, and perhaps the most obscure that awaits the attentions of the experimental biologist concerns the factors underlying the periodicity of its own activity.

CHAPTER VI

THE GENERAL CHARACTER OF THE MENSTRUAL CYCLE

OLD WORLD monkeys and apes, like man, differ from most lower mammals in experiencing a continuous series of monthly menstrual cycles in the absence of pregnancy. The difference is not one of kind, for the menstrual cycle, like the œstrous cycle, consists of a rhythmical series of morphological changes in the ovaries and accessory reproductive organs. It is, however, distinguished by a phase of endometrial destruction, lasting about four days, which results in uterine hæmorrhage and which is more pronounced and extensive than the cyclical endometrial degeneration of lower mammals.

The facts of reproductive physiology are of fundamental importance to the interpretation of the mechanisms of social behaviour. Unfortunately, although the nature of the œstrous cycle of lower mammals is fairly well understood, that of the menstrual cycle—because of the difficulty experienced in collecting the evidence necessary for its interpretation—is obscure enough to provide material for endless controversy. Apart from verbal statements, data about the human cycle can be gleaned only from operating and post-mortem tables. After painstaking and lengthy research, physiologists and clinicians have, however, accumulated the information necessary to elucidate some of its essential features.

The human menstrual cycle is calculated as beginning on the first day of one menstruation and lasting until the onset of the next. Ovulation occurs about midway between two hæmorrhages. It is thus possible to divide

the cycle into pre-ovulation and post-ovulation, or follicular and luteal phases. The endometrium, destroyed at menstruation, is regenerated in the first few days of the cycle. The end of the follicular phase, usually referred to as the "interval", is a resting period in which the mucosa is shallow and the glands are straight. The luteal growth phase of the endometrium begins when the corpus luteum is formed after ovulation, and ends at the next menstruation. During this stage the endometrium increases in depth, and its glands become sinuous and distended with secretion.

There is no external manifestation of the follicular phase in the human cycle. The vaginal smear technique devised for estimating the time of œstrus in rodents has yielded such conflicting results, that it is still uncertain whether or not women undergo a vaginal cycle. Moreover, generally speaking, human beings do not exhibit œstrous behaviour. The absence of any obvious signs indicative of the activity of œstrin represents the chief obstacle in the way of comparison of the human menstrual cycle with the reproductive mechanisms of the lower mammal.

Since they show clear indications of the follicular phase of the menstrual cycle, Old World monkeys and apes are in this respect intermediate between the lower mammals and man.* Many of them exhibit œstrous behaviour, and many manifest cyclical coloration and swelling of the skin around the external genital organs. And these changes, because they bear a definite relation to the maturation and rupture of the ovarian follicles, afford a valuable indirect means of inferring the ovarian phases. These phases can also be estimated by the vaginal smear technique, since a vaginal cycle is shown by all the animals of the group that have been studied. The occurrence of all these external signs greatly facilitates the analysis of the

* The main facts of the menstrual cycle of sub-human primates have been discussed in detail elsewhere. See Zuckerman [397, 398, 399]; Zuckerman and Parkes [401, 402]; Parkes and Zuckerman [283].

menstrual cycle. The task of comparing similar events in the menstrual cycle of primates and in the œstrous cycle of the lower mammals is also simplified by the relative ease with which physiological data can be collected both by observation and experiment.

The physiology of New World monkeys has not been studied, but a considerable amount of research has been directed towards the elucidation of the reproductive mechanisms of Old World primates. From the physiological point of view, the latter can be divided into two groups. The first comprises those species which do not show external cyclical changes. Their manifestations of reproductive activity appear to be identical with those of the human species. The second consists of those that exhibit cyclical swelling and coloration of the skin of the pubic region and buttocks. The spectacular character of these changes has made them subject to comment for hundreds of years. In many of the early pictures, apes and monkeys are shown with swelling of the pudendal region. Cuvier in his *Animal Kingdom*, published in 1834,[77] drew attention to the changes that are shown by monkeys belonging to the genus *Macaca*. He writes: "During the rutting season the labia pudendi, etc., of the females are excessively distended. . . . Hence the observation of Ælian that monkeys are to be seen in India which have a prolapsus uteri." In 1871 the same genus was singled out for note by Darwin,[78] who states that the female Rhesus macaque "has a large surface of naked skin round the tail, of a brilliant carmine red, which, as I was assured by the keepers in the Zoological Gardens, periodically becomes even yet more vivid, and her face also is pale red." In 1876, in a contribution to *Nature*, Darwin [79] laid emphasis on this phenomenon as a factor in sexual selection, comparing it with the bright coloration of the face and hindquarters of the male mandrill. To-day, that part of the body around the external genitalia which swells or shows colour changes during the menstrual cycle is usually referred to as the *sexual skin*.

The general plan of the menstrual cycle is much the same in all the primate species that manifest activity of the sexual skin. Menstruation occurs at fairly regular intervals of about thirty days. Immediately after its onset the skin around the external genital organs becomes red in colour and swells, reaching a maximum expansion before the middle of the cycle. Shortly after the mid-point the sexual skin suddenly resumes its quiescent appearance, in which state it continues until the onset of the next bleeding, when it again becomes active. This type of cycle is found in perhaps most Old World primates, its main variation being in the actual character of the changes occurring in the sexual skin.

Our present knowledge of the reproductive mechanisms of the apes is scanty. There has been little opportunity up to the present for studying the menstrual cycle of the gorilla. On the other hand, there are many superficial accounts of the reproductive mechanisms of the chimpanzee. In this animal the cycle lasts from thirty-four to thirty-six days.[217, 360] Menstrual bleeding continues for three to six days, and is followed by considerable swelling of the sexual skin, which involves the tissues around the anus and the vulva. About the middle of the cycle the swelling subsides, and the sexual skin remains quiescent until after the succeeding menstruation. There is no reliable record of the cycle in the orang, but it would seem that it is closely similar to that of the chimpanzee. Little information is available about the gibbon. According to Pocock[286] "the interval between the menstrual discharges is a little over the calendar month, and the discharge continues for two to three days." "The pudendal organs are always conspicuous by reason of their turgescence, and no very conspicuous change in their condition precedes the menstrual discharge."

Little is known about the reproductive activity of the langurs and guerezas, monkeys of the genera *Pithecus* and *Colobus*. According to Heape,[159] the only external

sign of menstruation, apart from bleeding, is slight swelling of the vulva and sometimes also of the nipples. The genus *Cercopithecus*, which comprises the African tree-monkeys or guenons, contains a larger number of distinct species than any other primate genus. The genus *Erythrocebus* is closely related and consists of a few species of the more terrestrial group of hussar monkeys. In almost all the species of these two genera thus far observed, the only external sign of the approximately thirty-day cycle appears to be menstruation itself. Cyclical variation does not seem to occur in the form or coloration of the perineal region. The only known exception is the Talapoin monkey (*Cercopithecus talapoin*), the smallest of the Old World monkeys. The time relations of the external changes shown by this animal are unknown, and observations of only one captive animal have hitherto been recorded.[397] In this animal, the pudendal organs, when quiescent, are inconspicuous, but when the sexual skin is active, the clitoris and the skin surrounding it expand into a lobe about an inch in diameter, and the skin surrounding the labia majora—laterally as far as the callosities, and posteriorly as far back as the base of the tail—swells into a series of folds. The colour of the sexual skin does not vary, and the transition from the quiescent to the swollen state and the return to the resting stage are slow.

Cyclical coloration and swelling of the sexual skin are very marked in the mangabeys (Genus *Cercocebus*). They have been recorded in the sooty mangabey (*C. fuliginosus*), in the white-crowned mangabey (*C. torquatus*), in the white-collared mangabey (*C. collaris*), and in the grey-cheeked mangabey (*C. albigena*).[287] The swelling begins either during or soon after the menstrual bleeding, and subsides about the middle of the cycle, which varies in length between thirty and forty days. At the height of swelling the sexual skin extends from the root of the tail to the clitoris, and consists of an upper and a lower rounded expansion

connected by a narrower area. The upper expansion is the swollen circum-anal skin ; the intermediate part between the callosities is the swollen vulva, while the lower part is the swollen clitoris. The entire swelling may be four inches in length (from base of tail to lower limit of clitoric swelling), two inches in width, and two inches in depth. The swelling is absorbed very rapidly about the middle of the cycle.

More has been written about the reproductive mechanisms of the Rhesus macaque than about those of all the other primates together. This monkey shows distinct cyclic changes in its sexual skin. Accounts of the external changes that occur, however, are somewhat conflicting. This is undoubtedly due to the fact that the more prominent change is one of colour rather than of swelling. Without any objective colorimetric standard it is almost impossible to be sure how much the hue of the sexual skin varies from one day to another. The sexual skin extends from the neighbourhood of the anal and vaginal orifices to the lower abdominal wall and the tail, continuing over the buttocks and down the backs and insides of the thighs. Occasionally, the legs may also be affected. Collings[70] describes the areas as being quite symmetrical in arrangement, with sharp borders that do not change from the "earliest blush to the very height of color," which is red and occasionally tinged with blue. The hair of the sexual skin area is sparse and, when activity of this area is at its height, the hairs stand on end. The degree of swelling that occurs is variable. During the inactive phase the sexual skin resembles the normal skin of the body, except that it is more like "goose flesh". In the active phase it becomes pouched and furrowed, and sometimes may even swell so as to resemble a series of confluent blisters. The actual amount of body surface that shows cyclical coloration varies in the individuals of a species, and in the same animal from cycle to cycle. Swelling and pouching is not obvious in all. The face may show cyclical colour changes that synchronize with the sexual-

skin cycles, and occasionally pronounced swelling of the skin just above the root of the nose may be noticed. Corner [72] found that the menstrual cycle of the Rhesus monkey varies about a modal length of twenty-seven days, the menstrual flow lasting from four to six days. Reports on the time relations of activity of the sexual skin are conflicting. Corner's opinion was that coloration

> "fluctuated, as to presence and extent, in a very capricious manner. . . . Once established, it sometimes persisted throughout several cycles, and at other times disappeared almost entirely after the menstrual flow. Once or twice, one day's time was sufficient to accomplish complete fading of the pigmentation and to reduce the inguinal pouches from the size of walnuts down to a few flabby folds of bluish skin."

Collings, however, found that the coloration of the sexual skin of *M. mulatta* "reaches its apex during the third week after the onset of menstruation and fades gradually as the time of the next menses approached". Allen also noticed that the cyclical coloration was most marked between the tenth and twentieth days of the cycle, which in his monkeys averaged thirty-nine days.[9]

Variations in colour and form of the sexual skin of the bonnet macaque have not been described. The cycle lasts roughly thirty days, and is characterized by a copious mucous vaginal discharge, which appears to be most profuse towards the middle of the cycle. The source of the discharge is the cervix—neck of the uterus —which is extremely glandular.

The length of the cycle in the common or crab-eating macaque is approximately the same as in other macaques. Reports about the activity of the sexual skin of this monkey are conflicting. Pocock,[287] formerly Superintendent of the London Zoological Gardens, remarked both in 1906 and 1925 on the absence of any cyclical coloration or swelling. Monkeys belonging to this species that are exhibited in the London

Zoological Gardens often show "scrotal" swellings, which do not appear to vary in size. Many fully-mature animals also manifest a swelling, which varies from time to time both in extent and colour, at the base of the tail. Spiegel [335] states that the sexual skin of this monkey shows a maximum of activity at the middle of the cycle, but according to Joachimovits, [199] the changes are most pronounced in the second half of the cycle.

The cycle in the pig-tailed macaque varies roughly from thirty to forty days. Conspicuous external cyclical changes occur in the pudendal skin, beginning either during or soon after menstruation and ending abruptly about the middle of the cycle. At the height of its activity the sexual skin extends from the clitoris in front to the tail behind. The skin in front of the pudendal cleft swells into an elongated pubic lobe, which includes the clitoris, while the pudendal margins and the skin surrounding the anus expand into a prominent, smooth, blue-red anal pad which extends laterally around the callosities.

Murie,[270] writing in 1872, gives a quaint description of the cyclical swelling in the Formosan rock macaque, which was figured by Sclater [310] in 1864. He writes that

> "in the female Rhesus Monkeys and the Baboons, at stated periods the hinder parts become unusually florid and puffy, but generally speaking the tumidity is restricted within reasonable bounds. In the case of the Round-faced Monkey, however, not only are the callosities and external genitalia swollen, but even the proximal end of the tail is inordinately increased in dimensions. In short, the whole of the posterior parts are literally a mass of deformity. The skin and subcutaneous tissues are frightfully distended, purple, deep red, and roseate, and here and there bagged out in great folds as if they were ready to burst from sanguineous and serous effusion. It is a hideous spectacle!"

Pocock describes the sexual skin of the Gibraltar ape as becoming turgid and slaty or purplish in tint during every menstrual cycle. "In the female of this species

the region of the rump above the anus rises into a high dome-shaped expansion, so that there is a long area between the anus and the generally externally invisible tail."

The cycle in the black "ape" of Celebes varies roughly between thirty and forty days, and striking changes occur in the sexual skin, which has a peculiar appearance, since the animal has only a short stump of a tail. At the height of swelling, which occurs towards the middle of the cycle, the under-surface of the tail is expanded, so that, with the circum-anal tissues, it forms a bright red spherical swelling that is continuous with an elongated vulval swelling.

Pocock states that cyclical variation does not occur in the condition of the genitalia or adjoining sexual skin of the Gelada baboons. In the species *Theropithecus gelada*, however, there exists, in both male and female, a bare spot on the chest and neck which is very brightly coloured. He writes:

> "The patch may be described as composed of two triangles reversely directed with their apices close together or confluent. . . . In the female where the two triangles are confluent, the shape of the patch may be likened to that of an hour-glass, and in this sex the patch is, as Garrod said, carunculated all along its lateral and inferior borders. These caruncles are ovate, flattened, and numerous, and, as I have been informed by Shelley, the keeper in charge of an adult pair of these animals recently exhibited in the Gardens, become enlarged during menstruation. *Theropithecus* is unique in the Cynomorpha in possessing this pectoral patch."

Among the keepers in the London Gardens the cyclically changing chest patch of the Gelada baboon is referred to as the "bleeding heart".

All the baboons and mandrills of the genera *Papio* and *Mandrillus* show pronounced external cyclical changes, more conspicuous than those of other monkeys or of apes. They have been described in the species *Papio porcarius*, the Chacma baboon; *Papio papio*, the Guinea baboon; *Papio anubis*, the Anubis baboon; *Papio*

hamadryas, the Hamadryas baboon, and *Papio cynocephalus*, the yellow baboon.[397]

The cycle of the Chacma baboon, the Anubis baboon, and the yellow baboon, usually varies between thirty and forty days. In Hamadryas baboons the average of seventy-two cycles observed in the London Zoological Gardens was 31·4 days, the range of variation being twenty-two to forty-six.[402] The sexual skin in this species begins to swell either during or immediately after menstrual bleeding, and is suddenly absorbed soon after the middle of the cycle. The duration of the period of growth, and the amount of swelling that occurs, are both somewhat variable, differing among individuals, and occasionally in the same animal at different times. In some species the maximum of swelling is reached in about a week, in others the skin continues to swell until the point when absorption suddenly begins. In the Hamadryas baboon the average duration of the phase of sexual skin swelling is about seventeen days; and that of sexual skin quiescence, which is less variable in length, fifteen days. The activity of the sexual skin bears approximately the same time relations in both the Anubis and the yellow baboons. The quiescent appearance of the perineal region varies in different baboons. Many show a residual swelling in the form of thick flabby folds of skin.

From its very beginning the swelling of the baboon is divided into two areas, a part anterior to the middle line of the vaginal orifice, composed of the clitoris and its sheath, and a hinder section comprising the posterior part of the vaginal orifice and the circum-anal skin. The anterior part swells into an oval-rounded body that does not overlap its attached base. The posterior swelling soon overlaps the line of its attachment, which passes medial to the callosities and immediately in front of the base of the tail. The swelling around the anus is several times larger than that of the clitoris, and both are very turgid, shiny, and bright red in colour. Some idea of the size of the swelling can be obtained from the

following measurements. In a small Chacma baboon the circum-anal lobe was twelve inches in transverse and vertical diameters and six inches deep, and the clitoric lobe was six inches long and four inches wide, while in a yellow baboon the circum-anal swelling was twelve inches in transverse diameter, nine inches in vertical diameter, and nine inches deep, and the clitoric lobe was about six inches long and three inches wide. It is a remarkable fact that the greater part of these relatively enormous swellings is usually absorbed within twenty-four to forty-eight hours. The initial decrease is very rapid.

The changes in the sexual skin are not manifested by any monkey or ape before puberty. The earliest definite sign of sexual maturity in the lower mammal is the first œstrus, which represents the culmination of a follicular phase of an œstrous cycle. The first definite sign of puberty in monkeys is activity of the sexual skin, which, as is indicated in the following chapter, corresponds to the first œstrus of the lower mammal. Thus the first effects of sexual maturity in both monkeys and lower mammals are due to the follicular hormone, œstrin.

Little is known of puberty in the gorilla. A young female investigated by Yerkes [395] was estimated to be six to seven years old when she died. She then weighed about 160 lb. and her dentition corresponded to that of a child about ten. She had never menstruated. The chimpanzee is said to reach maturity between the ages of eight and twelve. Yerkes and Yerkes, after critical examination of all available information, came to the conclusion that it "matures sexually slightly more rapidly than does man in the tropics". The chimpanzee, whose reproductive mechanisms are now being investigated in America, first menstruated at an estimated age of ten years.[360] Judging from my own observations of three female chimpanzees in the London Gardens, the process of puberty is very slow, and as much as two years may intervene between the first sign of activity of the sexual

skin and the assumption of the adult menstrual habit.* At first the animals undergo cycles of slight swelling unaccompanied by bleeding. The amount of swelling gradually increases during each cycle and after some months external bleeding occurs. The time relations of bleeding to swelling are at first different from those of the adult, and hæmorrhage is often prolonged. The manifestations of puberty in the orang have never been recorded. It is believed that it reaches sexual maturity at the age of eight years. The gibbon is said to pass through puberty at seven.

In the mangabey the first signs of sexual-skin activity may precede the first menstruation by several months. The age at which these monkeys attain puberty is unknown, but one animal belonging to the species *Albigena* had been two and a half years in the London Gardens before any activity of her sexual skin was noted. According to Hartman,[142] the Rhesus macaque reaches puberty at four years of age. Puberty is indicated by menstruation, which is preceded by sexual-skin coloration, and by "bag-like swellings" in the pubic region. These swellings are generally confined to the part that corresponds to the scrotum of the male. Hartman also notes that the menstrual cycle of younger monkeys are usually much more irregular than those of older females, both in their length and in the duration of their flow. My own observations show that this is a usual phenomenon in many species of sub-human primates.

There is no available record of the age at which baboons, drills and mandrills reach puberty. It is more difficult to judge the onset of puberty in a male than in a female, so that doubtful observational evidence of masculine sexual maturity is of little value unsupported by anatomical evidence. It may, however, be

* An interval of this length occurred in an animal (S), the first sign of whose puberty has been recorded elsewhere[397]. No data are available to establish whether or not she should be considered pathological. Comparable observations have been made of puberty in other primate species.

PLATE VIII

Photograph by F. W. Bond

MALE HAMADRYAS BABOONS DRINKING

(See p. 262)

noted that a young male Hamadryas baboon that has been four and a half years in confinement in the London Gardens does not appear to have reached sexual maturity. A female Chacma baboon that came into my possession three years after she had been caught showed no sign of swelling of the sexual skin until eight months had passed, when she must have been at least four years old. The inconspicuous swelling which marks the onset of puberty in the female baboon may persist with varying degrees of prominence for many months before menstruation occurs, and the first menstrual bleedings may continue for as long as a fortnight. In one young drill, at present living in the London Gardens, the sexual skin first showed signs of activity in November, 1929. Her cycles are still irregular (November, 1931), and the degree of swelling she shows is much less than that described for adults.

Thus all the available data suggest that the process of puberty is slow in apes and monkeys. The beginnings of sexual maturity are indicated in many species by coloration and swelling of the sexual skin, which does not attain adult proportions for some months. The first menstrual bleedings, which are usually prolonged and irregular, occur some time after the sexual skin becomes active, and, judging by dentition, at an age that is relatively younger than the corresponding human growth phase.

Monkeys that are seen in captivity have usually been caught when very young, and the average duration of their lives in confinement is not long. Many die from some acute or chronic infective disease either before or soon after reaching maturity. For this reason there have been fewer opportunities for observing the manifestations of pregnancy in sub-human primates than there have for observing those of puberty. Geoffroy Saint-Hilaire * found that the accurate determination of the duration of pregnancy in monkeys is extremely difficult, since they continue to copulate after conception. This

* Quoted from Breschet.[52]

opinion, expressed 100 years ago, has been confirmed by numerous other observers, and indirect methods have accordingly been devised for the estimation of the period of gestation, which in apes is believed to be about nine months, and which in monkeys is generally from five to six months. The sexual skin is in most species inactive during gestation. Fox,[116] however, records, without giving adequate details, that swelling occurred during the pregnancy of an orang that gave birth to a male baby in the Philadelphia Gardens on September 25, 1928. Montané's [260] observations indicate that the sexual skin is quiescent during pregnancy in the chimpanzee.

Both Heape [161] and Hartman,[142] on the other hand, state that the sexual skin of the Rhesus macaque is highly coloured during pregnancy. Hartman,[145] who has devised a sensitive test for determining the date of conception, gives the average of fifteen Rhesus macaque gestations as 164·3 days, the range being 149 to 174.

By observations of changes in the sexual skin,* I estimated the duration of pregnancy in a pig-tailed macaque as 171 days. The sexual skin did not swell during the pregnancy of this animal. By the same means the duration of six pregnancies of Hamadryas baboons in the London Zoological Gardens was estimated to be from 154 to 185 days, the average being 171 days. These figures are remarkably similar to those Hartman recorded for Rhesus macaques, and the 160 to 170 days which Spiegel [334] gives as the range of variation of pregnancy in the common macaque. The sexual skin was quiescent throughout these six pregnancies, and this represents the main difference between gestation in the baboon and in the macaque, in which the sexual skin retains its colour throughout pregnancy.

As a general rule, monkeys and apes devour the placenta. Nothing seems to be known of the reason for this behaviour, but the old view that the placenta stimulates milk secretion seems to be, as Hartman points out, fairly well-founded.

* See p. 103.

Monkeys and apes continue to nurse their babies for a very long period. Yerkes and Yerkes[395] consider that in the chimpanzee this period may extend to two years. This, however, may well be an underestimate, for there is definite evidence that young orangs continue to take the breast for a much longer time. An adult female orang was bought by the Zoological Society of London in January of 1928. When she arrived she was nursing a young animal, which was seen out of her arms only on rare occasions. Though the young orang was usually at the breast, it is unknown whether or not the mother was secreting milk. The baby died of tuberculosis two months after its arrival, and the most conservative estimate of its age, based upon its dentition, was four years. Brandes,[50A] of the Zoological Gardens in Dresden, also gives as his opinion that the orang continues to be nursed until it is about four years old. Monkeys do not nurse for so long a period. Spiegel found that the common macaque nurses its young and secretes milk for at least eighteen months. This is probably about the length of the nursing period for other monkeys. On the other hand, no more than about a month elapses before the young animal supplements its diet with solid food.

As a rule monkeys and apes do not show skin swelling nor do they menstruate during the earlier part of the nursing period. According to Montané,[261] this period of reproductive inactivity—usually called the *lactation interval*—lasts from eighteen to twenty-one months in the chimpanzee. In the first of two nursing periods of a pig-tailed macaque in the London Zoological Gardens it lasted eight months, in the second about six months. The end of the first was characterized by swelling of the sexual skin, while the end of the second was first indicated definitely by menstruation, although slight swelling had been noticed at least three months before the bleeding. In the Hamadryas baboon the lactation interval, during which there is no swelling, lasts for about five months. The only sub-human primate in

which activity of the sexual skin has been observed during the lactation interval is the Rhesus macaque, Hartman writing that a most brilliant colour is maintained for several weeks after parturition.[142]

The period of reproductive inactivity accompanying lactation follows parturition only if nursing takes a normal course. If suckling is abruptly discontinued during a lactation period (for instance, when the baby dies), or if lactation is not established (because the baby is still-born or dies soon after birth) only a short interval elapses before the onset of a menstrual cycle, which usually begins with swelling of the sexual skin. A chimpanzee that gave birth to a male in October of 1928 in the Philadelphia Gardens in America did not nurse her baby, which was removed after two days and artificially fed.[116] Vaginal bleeding occurred eleven days after parturition, and two days later her sexual skin began to swell. Five baboon babies have died in the London Zoological Gardens before the natural end of the lactation interval, and in every case the mother's sexual skin began to swell within ten to twenty days after their death.

The inactivity of the sexual skin during lactation is due, as is explained in the following chapter, to cessation of the normal cyclical activity of the ovaries and uterus.

CHAPTER VII

THE MORPHOLOGY, PHYSIOLOGY, AND INTERPRETATION OF THE MENSTRUAL CYCLE

THE baboon is the only sub-human primate whose ovarian cycle has been investigated in detail.[402] It has been shown, both by examination of animals that have died at known stages of the cycle, and by inference from the time of sexual-skin subsidence,* that ovulation occurs about midway between two menstrual bleedings.† No evidence that the baboon undergoes menstrual cycles without ovulation was obtained from the specimens studied—mostly field material. Ovulation seems to proceed alternately from the two ovaries, which always contain a large number of small resting follicles. At the onset of the follicular phase, a group of these begins to mature. The follicle that finally ovulates a fortnight later is the survivor of this group, the rest having degenerated. Immediately after ovulation the follicular cells of the ruptured follicle begin to swell and are transformed into luteal cells, which fill the shell of the ruptured follicle within a few days. The corpus luteum begins to retrogress about a fortnight after the beginning of its formation. Within a few days it is considerably atrophied, and by the time the next luteal phase is well-established—about three weeks later—the old corpus luteum can barely be recognized in sections of the ovary. The corpus luteum attains a greater size during pregnancy than at any stage in the cycle of the non-pregnant

* See p. 103.

† Both Corner [72] and Allen [7] have shown, by direct methods, that ovulation in the Rhesus monkey occurs between the tenth and fourteenth day following the first day of the preceding menses.

animal, the maximum development probably occurring in the second fortnight after conception. During the lactation interval the ovaries are altogether inactive, containing neither corpora lutea nor follicles above resting size.[402]

The endometrial cycle in monkeys closely follows the ovarian phases, and is almost identical with the series of rhythmical changes that occurs in the non-pregnant human uterus. The mucosa that is destroyed by menstruation is re-formed within a few days, and develops to the extent characteristic of the "interval" period. This "follicular" endometrium is much thinner than that of the luteal phase, and its glands are short and uncoiled. The endometrium grows extensively in the luteal phase that follows ovulation. Its depth increases, and its glands become coiled and begin to secrete. If conception does not take place, menstruation ensues suddenly about a fortnight after the animal has ovulated. The main anatomical effect of the menstrual process is necrosis of the inner two-thirds of the uterine mucosa. Regeneration begins while the necrosed tissue is still being shed and while bleeding is still proceeding from vessels that were involved in the degeneration of the endometrium. This is the picture of the endometrial cycle of monkeys when ovulation has proceeded normally. Heape,[159] Van Herwerden[365] and Corner,[73] as well as Allen,[9] have all shown that Entellus langurs, Rhesus monkeys and common macaques sometimes menstruate in cycles in which ovulation has not occurred. Such menstruation supervenes at the expected time, but from an "interval" endometrium. As no corpus luteum is formed in these cycles, the only uterine growth that occurs is that of the follicular phase. The amount of tissue destroyed at menstruation is therefore less in cycles without ovulation than in cycles with ovulation. It is important to recognize that the period of menstruation is the only time, in either type of cycle, when the uterine mucous membrane shows signs of degeneration. None occurs

at the time of ovulation. As Corner has pointed out, the endometrium of the monkey shows none of the "characteristic changes which mark œstrus" in the pig, rat, mouse, or guinea-pig. Degeneration of quite a different kind is seen in the uterus of a monkey killed during a lactation interval. The uterus is then much shrunken, and post-parturient degenerative changes can be observed both in the muscle layers and in the mucous membrane, which is even shallower than the interval endometrium of the normal cycle.

The cycle of changes in the vaginal wall is not so conspicuous in monkeys as in some lower mammals. Epithelial cornification is most pronounced, and epithelial cells are shed in greatest numbers, about the time of ovulation, while leucocytes are most numerous in the mucous membrane and in vaginal smears just before, during, and just after menstruation. Corner has shown that the occurrence or non-occurrence of ovulation does not affect the vaginal cycle of the Rhesus monkey. Epithelial cells and leucocytes are not the only cellular elements observed in vaginal smears from monkeys. Hartman,[144] who employs the vaginal smear technique for estimating the fertile period of the cycle, has recovered red blood cells from the vagina of the macaque at times other than menstruation, usually between the seventh and eighteenth day of the cycle. This "mid-interval bleeding", as it has been termed, may last for a considerable time. In one monkey it continued from the eighth to the eighteenth day. Without giving any evidence to support his view, Hartman has suggested that the "mid-interval" bleeding of the Rhesus monkey corresponds to the bleeding that results from the œstrous degeneration of the endometrium of the bitch. Tinklepaugh and Van Campenhout,[360] who have reported on the cyclical variations in the vaginal contents of the chimpanzee, were unable to corroborate this view. Using Hartman's technique, these observers found small numbers of red blood cells in the vaginal contents at such irregular intervals that it was impossible

to correlate their presence with any known uterine or ovarian event.

Very little is known about the cycle of changes that occurs in the mammary gland of sub-human primates. The size of the baboon mammary gland does not vary much during the menstrual cycle. The main part of the growth that transforms it into a functional organ occurs immediately after parturition, and it may then continue in an active condition, if it is stimulated by a series of pregnancies and periods of nursing. The gland atrophies rapidly when sucking is discontinued. It is interesting that the mammary gland had already begun to develop in a chimpanzee that died in the London Zoological Gardens before it had shown any manifestations of puberty.

The physiological factors underlying the anatomical changes in the accessory reproductive organs of monkeys are probably the same as those responsible for the cyclical changes that occur during the œstrous cycle of lower mammals. The times when the sexual skin is coloured and swollen suggest that it is immediately activated by the follicular hormone, œstrin, and that its manifestations are part of the follicular phase of the cycle. On such a view the swelling of the sexual skin in the baboon is analogous with the swelling of the ferret's vulva at œstrus. The change in the ferret has been proved, both by observation and experiment, to be a manifestation of the follicular phase.

In 1926 Allen[8] discovered that external cyclical changes do not occur in the sexual skin of ovariectomized adult Rhesus macaques, in this way proving that the activity of the sexual skin is directly controlled by the ovaries. He also showed that the sexual skin of these spayed females can again be activated by the injection of œstrin, and that a similar result is achieved by injecting the hormone into both normal and spayed immature Rhesus monkeys. Both he and Hartman[139] have also proved that abnormally long persistence of sexual-skin activity in the Rhesus monkey may be

due to the presence of cystic follicles in the ovaries. The sexual skin very soon resumes its quiescent appearance if these are artificially ruptured. These facts suggest that normal cyclical sexual-skin activity is the result of the stimulus of the follicular hormone. This becomes operative at the onset of a menstrual cycle, with the beginning of follicular growth, and is apparently removed about the middle of the cycle, usually when the follicle ruptures. The end point of sexual-skin activity in the Rhesus monkey is commonly described as occurring after the time of ovulation. This observation may be ascribed either to the difficulty of defining limits to the activity of the sexual skin, or to the possibility that the follicular hormone remains operative after ovulation.

The conspicuous change in the sexual skin of the baboon is not colour, but swelling. The abrupt absorption that occurs shortly after the middle of the cycle suggests that this change is correlated with some ovarian event, and observation has proved that sexual-skin subsidence coincides with ovulation. Three baboons that died in the London Gardens in the period of sexual-skin absorption had recently ruptured follicles in their ovaries. Two that died at the height of swelling showed mature follicles, while two that died in a phase of sexual-skin quiescence showed fully developed corpora lutea.[397, 402] As in the case of the Rhesus monkey, the fact that swelling of the sexual skin in the baboon occurs during the follicular phase of the cycle suggests that it is due to the activity of the follicular hormone œstrin. This inference has been confirmed experimentally. Œstrin injected into an ovariectomized baboon induces swelling that does not differ from the swelling of the normal animal.[283]

Allen's experiments on ovariectomized Rhesus macaques have proved that a decrease in the amount of œstrin injected is followed within a day or two by diminution in the activity of the sexual skin.[9] This observation indicates that the degree of sexual-skin

activity at any given time depends mainly upon the amount of œstrin being secreted or injected at that time, and that the maintenance of sexual-skin swelling depends upon the continued secretion of œstrin. The facts of the normal cycle of the sexual skin therefore suggest that the amount of œstrin secreted increases from the beginning of the cycle, to reach a constant, in some monkeys, about the middle of the pre-ovulation stage, and in others, for instance the Anubis baboon, at a later stage in the follicular phase. Less œstrin is secreted in the baboon at the beginning of sexual-skin swelling than at the time of maximum swelling, and the effects of the hormone become more intense as the wave of follicular growth proceeds in the ovaries. Enormous amounts of œstrin are needed to produce complete swelling of the sexual skin. Considering a unit of œstrin as the amount necessary to produce œstrous vaginal cornification in the mouse, sixty thousand to eighty thousand such units are required to produce full sexual-skin swelling in the baboon. On a weight for weight basis this is strictly comparable with the amount necessary to cause the uterine œstrous change in the mouse—200 mouse units. Though the sexual skin is not swollen either during the luteal interval between ovulation and menstruation or during pregnancy and lactation, there is no reason for assuming that the hormone is ineffective during these phases. The highly coloured sexual skin of the pregnant Rhesus monkey indicates that œstrin may be secreted during a luteal phase. The same conclusion is suggested by the fact that sexual-skin activity continues in the Rhesus monkey until the twentieth day of the cycle, and also by the fact that the sexual skin of baboons is often not completely absorbed after ovulation. During the luteal phase of a menstrual cycle, the sexual skin of many baboons is far more prominent than the pudendum of an ovariectomized baboon. Observations on a pig-tailed monkey in the London Gardens also show that the normal rate of œstrin secretion may be sometimes

disorganized. The sexual skin of this animal remained swollen throughout one cycle, while on another occasion she experienced a cycle without any sexual-skin swelling. It is also interesting to note that the first of two lactation intervals in this animal ended with conspicuous sexual-skin swelling, while the sexual-skin swelling that marked the close of the second was almost imperceptible.

The similarity in the time relations of activity of the sexual skin throughout the group of Old World primates suggests that the same physiological mechanism operates in all. It may be safely inferred that most, if not all, Old World primates ovulate about the middle of the menstrual cycle, and that œstrin is the responsible factor underlying the swelling and coloration of the sexual skin throughout the group.

Œstrin has a characteristic effect upon the atrophied uterus and vagina of the ovariectomized Rhesus monkey, inducing extensive growth in both these organs. The vaginal wall thickens, its epithelium becomes cornified, and leucocytes disappear from the vaginal smears.[9] The amount of growth induced in the uterus never exceeds the amount that occurs during the follicular phase of a normal cycle.[13] Full pre-menstrual development of the endometrium cannot be obtained even after the administration of large amounts of œstrin. Shortly after the cessation of injections, leucocytes reappear in the vaginal contents, the uterus resumes its atrophied size and endometrial bleeding occurs.[13]

Full pre-menstrual growth can be induced in the ovariectomized monkey only by administration of corpus luteum extract. This experiment has been performed by Hisaw, Fevold and Meyer,[174] who injected œstrin before applying their corpus luteum preparations, having discovered that the effects of the corpus luteum are inhibited if large amounts of œstrin are simultaneously injected. The latter observation seems to explain the negative results obtained by Robertson,[296] who failed to induce pre-menstrual growth with parallel

applications of the follicular hormone and corpus luteum. Several investigators have shown that previous treatment with œstrin is almost essential for the production of the effects of corpus luteum in the endometrium of the rabbit.

The recent researches carried out by Hartman and his co-workers on the effects of extracts of the anterior lobe of the pituitary on the reproductive cycle of monkeys have led to very important conclusions. Hartman has shown that if anterior lobe substance is implanted into a Rhesus monkey, the uterus and ovaries enlarge, and their activity is increased.[152] In collaboration with Firor and Geiling, Hartman has also shown that the pituitary is probably responsible for the menstrual process.[155] Experimental removal of the pituitary in the monkey leads to atrophy of the reproductive organs and disappearance of menstrual cycles. The injection of œstrin into an animal deprived of its pituitary gland has no effect, although œstrin causes bleeding when injected either into spayed or normal monkeys. The administration of extracts of the anterior lobe of the pituitary in any form results in endometrial bleeding "whether the animal be normal, sick and amenorrheic, castrated or hypophysectomized, old or young." The uterine bleeding produced in this manner is not accompanied by growth or congestion of the uterus and ovaries. Hartman and his co-workers conclude that menstruation "is due to a hormone elaborated by the anterior lobe separate and distinct from that of growth, follicle stimulating (Smith and Engle), luteinizing (Evans and Simpson), or thyroid activating (Smith; Crew and Wiesner). We might with reserve speak of a fifth anterior-lobe hormone."[156]

Though as yet uncorroborated, these experiments are sufficiently convincing to lend definition to the questions that require answer if the menstrual cycle is to be satisfactorily explained in terms of the œstrous cycle of the lower mammal. Two sets of problems relating to the reproductive mechanisms of the primate

must be distinguished. The first concerns the actual cause of the uterine destruction, manifested as menstruation, and intervening between successive menstrual cycles. This necrotic process occurs in the lower mammal as well as in man. Both the endometrial degeneration of the monkey and the destruction that takes place in the rat's endometrium at the end of pseudo-pregnancy may be effected in the same way. The second set of problems concerns the cyclical endometrial growth changes occurring in monkeys and apes. It is necessary to consider in what anatomical and physiological ways these rhythmical phases correspond with those of the lower mammal.

Menstruation is usually explained as being due either to the operation of some excitatory factor or to the removal of some previously active stimulus. The classical theory of the human reproductive cycle, based upon the work of Fraenkel, Hitschmann and Adler, Meyer, and Schroeder, is an explanation of the latter kind, and is well summarized by Corner.[73]

> "Ovulation is a periodic function occurring regularly at about the middle of the interval between two menstrual hemorrhages. It is followed by the development of a corpus luteum at the site of the discharged follicle; and this structure, acting as a gland of internal secretion, causes changes in the endometrium (the well-known 'premenstrual' changes first described by Hitschmann and Adler) by which it is prepared for implantation of the embryo. If the ovum is fertilized the 'premenstrual' endometrium thus becomes the endometrium of early pregnancy. If, however, the ovum is not fertilized, the corpus luteum retrogresses, and at about the same time the 'premenstrual' endometrium suddenly breaks down with resultant hemorrhage. Menstruation is on this theory merely a violent demolition of the 'premenstrual' uterine edifice, some days after the expected tenant (the embryo) fails to arrive. Each menstrual period is therefore necessarily dependent on the occurrence of ovulation about two weeks before."

As Corner first pointed out, this theory is incorrect because it implies that the development and

retrogression of a corpus luteum, and the growth of a luteal or premenstrual endometrium, are essential for menstruation. Actually menstruation may take place, in both monkeys and women, without the previous occurrence of ovulation and the consequent formation of a corpus luteum and a "premenstrual" endometrium. An equally serious limitation of the clinical theory is its complete disregard of the existence of a follicular phase—of effects due to the activity of the hormone called œstrin—in the human menstrual cycle. This internal secretion is undoubtedly elaborated in the human body, since it can be extracted in large quantities from the urine and the placenta.

An alternative theory of the cause of menstruation, suggested by both Allen (1927)[9] and de Jongh and Laqueur (1931),[89] centres round the effects of œstrin. Their hypothesis overlooks the important effects which the corpus luteum, as an organ of internal secretion, has upon the human cycle. It suggests that menstruation may be due to the removal of the stimulus of the follicular hormone after it has been functioning for a certain time. Allen formerly assumed that the follicular hormone is responsible for all the uterine changes of the menstrual cycle, as well as for those of pregnancy. In the lower mammal the stimulus of the follicular hormone is normally removed at the end of the phase of follicular growth in the ovaries—that is to say, at ovulation. Endometrial destruction—pro-œstrous or œstrous degeneration—synchronizes with its removal. In order to explain the fact that menstruation is normally delayed in monkeys for some two weeks after ovulation, Allen suggested that in them the secretion of the follicular hormone does not cease at ovulation. In extension of this view he suggested that the hormone is produced by the corpus luteum in the second half of the cycle. There is no evidence to support this view, which conflicts with most of the relevant facts. The identity of the corpus luteum as a separate organ of internal secretion has been

adequately proved by recent experimental work. It is the chief agent underlying the formation of the premenstrual endometrium. The experimental evidence upon which Allen relied for support of his view is that uterine bleeding follows the cessation of injections of œstrin into ovariectomized monkeys. Hartman's recent experiments suggest, however, that this is not a direct effect. The bleeding appears to be dependent upon the presence of the anterior lobe of the pituitary gland, since cessation of œstrin injections into monkeys from which the pituitary has been extirpated is not followed by uterine bleeding.

Shaw,[318] amongst others, has put forward the view, that menstruation is due, not to the removal of a stimulus, but rather to the operation of some additional factor. Hartman's experiments seem to lend practically all the support required for the proof of this hypothesis. Menstruation appears to be determined by some substance elaborated by the pituitary gland, and not, as was formerly thought, by the ovaries. Further experiment is necessary, however, before it can be stated that menstruation is due to the application of a hormonic stimulus from the pituitary gland, rather than to the removal of a previously effective stimulus of the same gland.

The second set of problems relating to the interpretation of the primate menstrual cycle has been defined as concerning the homology between the cyclical growth changes of the endometrium in primates and those in lower mammals. The need for distinguishing between these problems and those involving the factors underlying the menstrual process has only recently become evident. The relevant facts may be briefly summarized before entering upon this discussion.

The lower mammalian œstrous cycle, for instance that of the bitch, may be divided into a follicular and a luteal phase. The follicular phase culminates in œstrus at the time of ovulation. In the earlier, or pro-œstrous, part of this phase, follicles mature in the

ovaries, and the uterine mucosa grows moderately. The slightly hypertrophied endometrium degenerates at œstrus, the time of ovulation. This change is frequently referred to as pro-œstrous uterine degeneration or destruction. Corpora lutea develop after ovulation and, under their influence, the uterine mucous membrane undergoes a second phase of growth, usually termed the phase of pseudo-pregnancy. The pseudo-pregnant period, like the pro-œstrous stage, ends with a phase of uterine destruction. There are thus two phases of destruction in the reproductive cycle of the lower mammal, and two phases of uterine growth, separated from each other by the period of pro-œstrous uterine degeneration.

In the menstrual cycle there is only a single phase of uterine destruction, occurring at what is usually the end of the luteal or pseudo-pregnant period. There is no endometrial degeneration at the middle of the cycle when ovulation occurs. Ovulation does not, however, take place in every cycle, but even in its absence menstruation follows at the normal time. The endometrial growth occurring in the pre-ovulation or pro-œstrous part of the cycle is slight. If ovulation does not take place, this represents the only growth phase of the uterus, and the menstrual process destroys only this "interval" endometrium produced by the growth of the earlier half of the cycle. If, on the other hand, ovulation does occur, the subsequent formation of a corpus luteum determines a post-ovulation growth phase in the uterus, a "pre-menstrual" endometrium being formed. This is subsequently destroyed by the menstrual process. The activity of the follicular hormone is manifested externally, mainly in the earlier half of the cycle, by swelling of the sexual skin.

Marshall's interpretation of the events of the menstrual cycle has attracted considerable notice.[251] He has suggested that the pro-œstrous or follicular endometrium in the primate becomes merged with the

PLATE IX

Photograph by J. E. Saunders

A GROUP OF HAMADRYAS BABOONS FEEDING

(See p. 262)

pseudo-pregnant or luteal mucous membrane. In the bitch they are separated by pro-œstrous destruction. Though this view appears to be substantially correct, details of his explanation conflict with the facts. His description implies that menstruation represents the breakdown of the pro-œstrous uterine growth which heralds the succeeding ovulation, combined with, (in his own words "telescoped into"), the breakdown of the pseudo-pregnant endometrial growth which followed the preceding ovulation. This means that the follicular phase or pro-œstrus comes to an end at the very beginning of a menstrual cycle, and that an interval of at least ten days elapses between the end of pro-œstrous destruction and the ovulation which follows. Actually the follicular phase or pro-œstrus continues at least throughout the earlier half of the menstrual cycle, as the changes in the sexual skin show.

Hartman's interpretation of the cyclical growth changes in the uterus hinges upon his discovery in the Rhesus monkey of red blood-cells in vaginal smears between the seventh and eighteenth days of the cycle—the phenomenon he has termed "interval" bleeding. He writes:

> "Ovulation takes place almost exactly in the middle of the menstrual cycle, counting from the first appearance of the menstrual flow. Under the influence of the expanding graafian follicles, growth of the endometrium is initiated and congestion produced, resulting in slight extravasations of blood into the mucosal stroma and probably diapedesis into the uterine cavity. After ovulation, under the influence of the corpus luteum, the premenstrual growth and swelling of the endometrium take place. In the absence of fertilization of the ovum, and on the consequent degeneration of the corpus luteum, the hypertrophied functionalis desquamates and the menstrual hemorrhage results." [146]

On this view the menstrual cycle is directly homologous with the œstrous cycle of the bitch—the "intermenstrual bleeding" being the "homologue of pro-œstrum in the dog", the endometrial destruction that

occurs at the time of ovulation. When this was written, Hartman apparently accepted the clinical view that the retrogression of the corpus luteum is responsible for menstruation. His own researches have since helped to disprove this hypothesis. Apart from this, there are serious objections to his interpretation of the homologies of the primate endometrial phases. As yet no evidence has been provided to substantiate his belief that the "interval" bleeding in the macaque originates in the uterus. This view conflicts with the fact that histological studies of the endometrial changes in both women and monkeys have failed to reveal signs of uterine bleeding or degeneration occurring at any time other than the true menstrual periods. The œstrous degeneration in the uterus of the lower mammal is not represented in the menstrual cycle of primates. Moreover, as has already been mentioned, the comparable bleeding in the chimpanzee does not show the same time relation, nor does it suggest a correlation with any definite ovarian event. Hartman's explanation also implies that follicular effects are confined entirely to the pre-ovulation phase of the menstrual cycle. This, too, conflicts with the facts. Data have been recorded on page 105 which indicate that follicular changes may continue throughout the cycle.

Elsewhere I have suggested a different interpretation of the primate reproductive cycle.[397] According to this view, in cycles in which ovulation occurs, menstruation represents a delayed breakdown of the follicular endometrial growth which heralds ovulation, combined with the destruction of the pseudo-pregnant growth which follows the *same* ovulation (see Diagram 1C). In cycles in which ovulation does not take place, menstruation represents only the delayed degeneration of the pro-œstrous or interval endometrium (see Diagram 1B). This explanation implies that the regeneration of the uterine mucosa following menstruation and its transition to the "interval" type of endometrium is comparable with the pro-œstrous endometrial

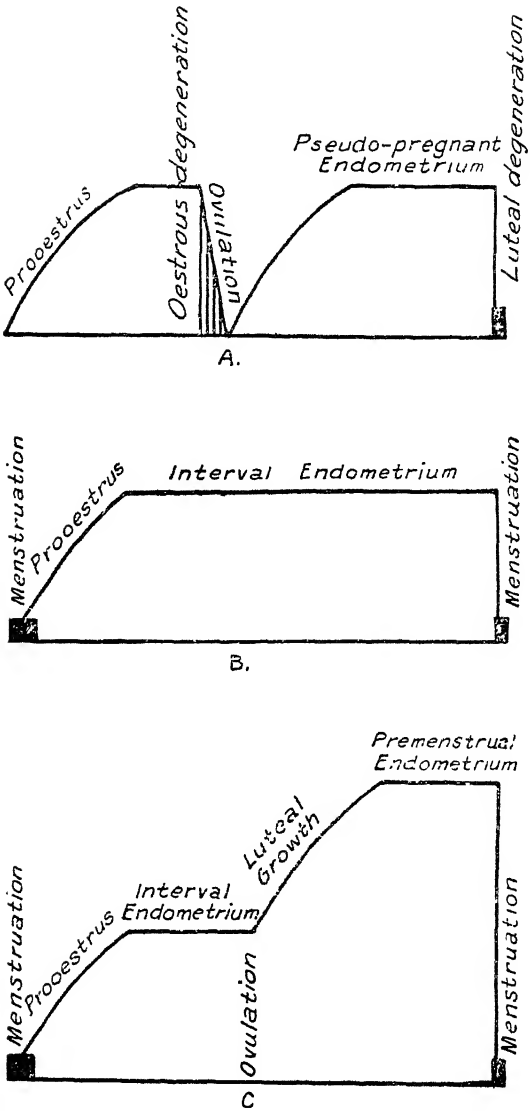
growth which occurs in the lower mammal (see Diagram 1A). The prolongation of sexual-skin effects through the luteal phase of the cycle * implies that the follicular hormone is to some extent effective throughout the primate menstrual cycle.

The sequence of events in the primate menstrual cycle appears to be as follows. Œstrin is secreted in increasing quantities throughout the first fortnight. It produces changes in the sexual skin, and growth in the endometrium (not exceeding that characteristic of the "interval" stage). About the middle of the cycle the amount secreted abruptly diminishes. Since sexual-skin changes do not disappear completely, it is possible that the œstrous hormone operates at a lower level of activity until the cycle ends with menstruation about two weeks later. The post-menstrual growth of the endometrium and its transition to the "interval" stage is comparable to the pro-œstrous uterine growth of the lower mammal. If ovulation does not occur, the endometrium does not continue to develop after the middle of the cycle. The animal menstruates a fortnight later from an "interval" endometrium which has been produced by the follicular hormone. When ovulation occurs (at about the middle of the cycle) the subsequent development of a corpus luteum determines a further phase of growth, which is superimposed on the follicular "interval" endometrium. The uterine mucous membrane now becomes "pre-menstrual" in type. If conception does not take place, the corpus luteum retrogresses about fourteen days after ovulation, and the "pre-menstrual" endometrium, apparently in response to a stimulus from the anterior pituitary, breaks down. Menstruation therefore represents both pseudo-pregnant destruction and a *delayed* pro-œstrous degeneration in the ovulating non-pregnant female primate.

According to this view, the main difference between the menstrual cycle of the primate and the œstrous cycle of the lower mammal lies in the distribution

* See pp. 92, 103, 105.

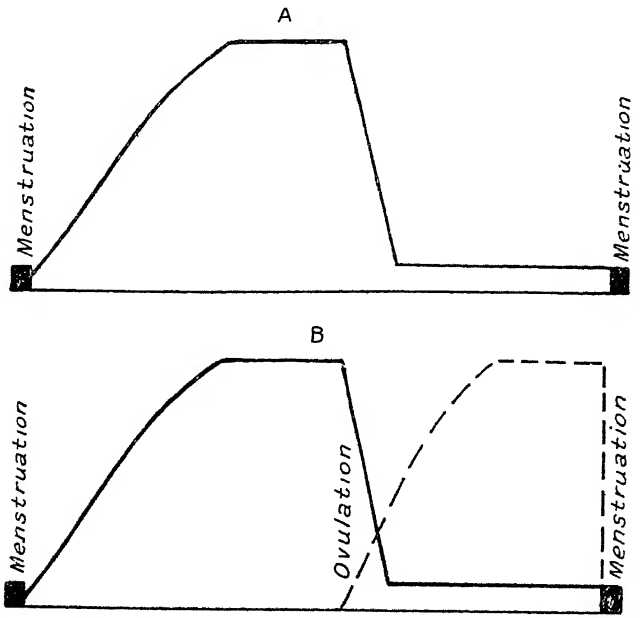
DIAGRAM 1.



Schematic representation of the endometrial changes in the œstrous cycle of A, the dog: B, the primate (cycle without ovulation) C, the primate (cycle with ovulation).

of their respective follicular phases. It is generally believed that in a lower mammal such as the bitch, the follicular phase ends abruptly with pro-œstrous destruction, and does not extend into the ensuing luteal phase (see Diagram 1A). The endometrium of pseudo-pregnancy is built up, under the influence of

DIAGRAM 2.



Schematic representation of the phases of the primate menstrual cycle. Unbroken line the variation in the effects of the follicular hormone. Broken line: the variation in the effects of the corpus luteum. A. Cycle in which ovulation does not occur. B. Cycle in which ovulation occurs.

luteal hormones, from an endometrium that has undergone degeneration at the time of ovulation. Very few instances of follicular effects occurring during the luteal phases of lower mammals have been recorded (see page 78). Moreover, the behaviour of the lower mammal is a further indication of the rarity of any such occurrence. On the other hand, the follicular

phase of the primate cycle, though its main effects occur in the earlier half, is prolonged over the entire cycle (see Diagram 2A), and pseudo-pregnant growth is *superimposed upon* a persisting pro-œstrous endometrium maintained apparently by the follicular hormone (see Diagrams 1C and 2B).

If this interpretation be correct, the differences in sexual behaviour between the primates and the lower mammals reflect their different sexual physiological mechanisms. The matings of the lower mammal are confined to short periods that appear to be circumscribed by activity of the follicular hormone. The matings of the primates are diffused over the entire cycle, coinciding with the continued action of the follicular hormone, but varying in frequency according to the varying degrees of activity of that hormone.

CHAPTER VIII

THE ŒSTROUS CYCLE AND BEHAVIOUR

EVERY phase of the œstrous cycle is reflected in a characteristic pattern of social behaviour. The movements that occur in an animal society are the final responses emerging from the interaction of three different groups of factors—the separate physiological conditions of its members, the stimuli inherent in a varying environment, and the mutual stimuli presented by the animals themselves. A complete account of an animal's life would contain a full description of the physiological background of its patterns of "unconditioned" or native reactions, as well as the history of its continuous adaptation to a varying external world. The œstrous cycle is important from this point of view, not only because it is responsible for the most striking internal changes affecting the disposition of the female animal, but because it is responsible for presenting to the male some of the most powerful stimuli with which he comes into contact.

Since the activities of any one member of a society constitute a collection of stimuli to whose influence every other member is exposed, it follows that any variation in the behaviour of a single member of the group will affect the others in the group. The reproductive phase of any one animal is responsible, therefore, not only for the behaviour of that animal, but also for certain of the responses of its fellows. For example, a female in œstrus attracts the attention of males, who, in the process of pursuit, come into contact with one another. Usually they respond pugnaciously to this new situation. The dominant male

eliminates the others and mates with the receptive female, the group assuming a different state of balance as soon as she passes out of œstrus. When it is considered that generally not one but many females are effective in stimulating movements within a society, some idea is obtained of the complexity of the reactions that are determined by the varying reproductive phases of its members.

In his classification of reproductive phenomena, Heape in 1900[165] defined "œstrus" as the "special period of sexual desire of the female." It is then that "the female is willing to receive the male and fruitful coition rendered possible in most, if not in all, mammals."

He also defined a condition of "abnormal œstrus" to include those instances in which female mammals receive the male when not in the true, or physiological, œstrous condition. The two types of œstrus are distinguished from each other by the fact that true œstrus is always related to certain specific uterine and ovarian changes, whereas abnormal œstrus may occur at any time. The emphasis that Heape laid upon these two kinds of feminine mating response is noteworthy, even though his definition of "abnormal œstrus" is vague. It is important because it draws attention to a physiological fact—the fact of the relation between physical œstrous changes and œstrous behaviour. Unfortunately, Heape did not indicate which mammals exhibit abnormal œstrus. He simply stated that "this condition may occur in various mammals during pregnancy, and has frequently been noticed in most species of domestic mammals during that period, while it is evident in a considerable number of animals also at other times." The prevailing view at the present time is that this is very rare. Thus Hammond[137] writing in 1925 states that "the domestic rabbit differs from all other animals except man in that coitus is allowed during pregnancy."

Since œstrous behaviour in the female has so far-

reaching an effect in any society, it is of especial interest to understand the nature of the anatomical and physiological factors underlying the œstrous condition which makes a female receptive of the attentions of potent males, and to analyse the nature of the effective stimulus to which the males respond by pursuit and mating. The conjugal act, as Stone [338] writes, "involves both a masculine and a feminine pattern of activity, the elements of which have a relationship of functional interdependence" appearing in serial and synchronized order, so that the elements of one pattern act in harmony with those of the other.

Several lines of research suggest that the behaviour of the female mammal at œstrus may not be dependent upon the presence of ripe and distended follicles in her ovaries. The greater number of follicles are found in the peripheral or cortical layer of the ovary. Blair Bell found that œstrus reappeared in ovariectomized rabbits, after decorticated ovaries had been grafted into them.* This experiment indicated that ripe follicles are unnecessary for the production of œstrus. Brambell, Fielding, and Parkes, by means of X-rays, destroyed the entire ovarian follicular system in mice.[281] They found that the animals continued to undergo œstrous cycles after the operation. This experiment, which has been confirmed by other observers, again proved that the maturation of follicles is not essential for the production of œstrus. Different results were obtained, however, when the experiment was repeated, using guinea-pigs instead of mice. Genther [124] found that distended follicles were present in the ovaries of those of her guinea-pigs that continued to undergo œstrous cycles after irradiation. It is therefore conceivable that in this animal the factor underlying œstrous behaviour may be distended follicles. Zondek has shown that follicles may mature in the ovaries of mice without producing œstrous effects. By adding thallium compounds to the food of mice, he suppressed

* Quoted from Parkes.[281]

all cyclic changes, without affecting the ovaries. Follicles continued to mature and rupture, and corpora lutea developed in a normal manner.*

The only known anatomical changes characteristic of œstrus are maturation of follicles in the ovary and growth changes in the other reproductive organs. Since the experiments described above suggest that the condition of œstrus may not necessarily depend upon the presence of distended follicles, it is possible that œstrous behaviour is determined by changes in the uterus and vagina. Mating would be impossible for some mammals if vaginal œstrous changes did not occur. Except at œstrus the vaginal orifice of the guinea-pig is closed by an epithelial membrane. Its destruction forms part of the normal pro-œstrous anatomical changes. Many physiologists, in consequence, regard the vaginal cornification that occurs in most mammals at œstrus as a change designed to facilitate copulation. Nevertheless, the vaginal change does not seem to be the important factor underlying the demeanour of the œstrous female. Very little œstrin is needed to produce the vaginal reaction in an ovariectomized mouse. About 400 times as much is necessary for the induction of copulatory receptivity, and the same amount is required to produce œstrous distension of the uterus. Not only is the reaction threshold of the vagina so much lower than that of the uterus and of the mating response, but the vaginal cornification reaction is indeed not a specific characteristic of œstrus. It may occur in certain deficiency diseases unaccompanied by the characteristic pattern of œstrous behaviour.[281] Thus the vaginal reaction does not appear to have any specific connection with œstrous behaviour. There is no evidence to show whether or not the uterine change has any closer relationship.

Œstrus forms only the last part of the follicular phase. This means that in lower mammals the period of mating is not confined to the period of the

* Quoted from Parkes.[281]

activity of œstrin, but only to the latter part of that period. It was pointed out in Chapter VII that in the lower mammal the physiological action of œstrin ends in effect with the endometrial degeneration and vaginal cornification that occur about the time of ovulation. The anatomical condition of œstrus represents the destruction of the mucosa that has been built up under the influence of œstrin, in the earlier part of the follicular phase—the pro-œstrous period. Therefore it seems that, although œstrin might be called the mating hormone, its effect in the lower mammal is only cumulative, and that the female is receptive only after the hormone has been acting for some time. It is clear why this is so in the guinea-pig, since its vagina becomes permeable only towards the end of the follicular phase when its closure membrane is ruptured. But it is difficult to understand why receptivity should be restricted to the last period of the follicular phase in the dog, an animal whose vagina is always permeable. It is possible, however, that œstrous behaviour is determined by a cumulative effect of œstrin upon the neurological elements of the particular motor mechanisms involved in mating responses. But these are matters for speculation. Our knowledge of reproductive phenomena does not yet extend to an explanation of the correlation between the morphological and physiological changes of œstrus and fixed patterns of overt behaviour which depend upon neuro-muscular mechanisms.

The mating stimulus inherent in the œstrous female is effective only upon potent males. Neither œstrous nor anœstrous females stimulate immature males into copulatory activity. According to Stone [338] the copulatory act in the albino rat is an organized unit of behaviour that runs its course smoothly when the first of the series of its component elements is set into action. Some of the elements of the act are never exhibited before copulation is first effected, while those that may possibly be observed before puberty have no

obvious connection with it till they are actually incorporated in it. The initial copulatory act of the young male is, indeed, almost indistinguishable from the mating behaviour of the experienced adult. It seems, therefore, that whatever the nature of the effective œstrous stimulus may be, it operates only in the mature male rat, an organism already changed by the reproductive processes underlying puberty.

Detailed analysis has been made of the nature of the œstrous stimulus to which the male responds. It is well known that potent males react differently to anœstrous and œstrous females. The bitch in heat is a magnet for all dogs in her neighbourhood. Rams wander in and out of a flock of ewes, stopping to mate with those in heat. As the social and sexual pursuits of most common mammals are accompanied by much sniffing, there is a common belief that the male lower mammal "smells out" the female in heat, and that an olfactory stimulus activates sexual impulses. But as Stone points out, when one animal sniffs another, both experience, in addition to olfactory perceptions, a large amount of cutaneous stimulation which in itself might provoke the exhibition of sexual behaviour. It is therefore impossible to determine by superficial analysis the particular stimuli most effective in evoking sexual responses. Moreover, experiment has proved that the traditional view regarding smell has no real foundation, even though it may still be perfectly true that masculine interest is actually associated with an alteration in the female's olfactory quality, which is due to the products of degeneration of the pro-œstrous growth of the mucous membrane of the generative tract.

If a non-œstrous female albino rat is put into the cage of a potent male, she almost immediately begins to explore her new surroundings, closely followed by the male, who devotes himself to a close examination with his snout of her ano-genital region. If he is too vigorous in his attentions, she may resist by kicking,

or she may retire to a corner where she is more protected from his assaults. The œstrous female behaves differently. Her tour of exploration is much more restricted, and as soon as she is approached by the male, she takes up a tense attitude that may be accompanied by general shivering. After the male has spent a moment smelling and licking her, she runs briskly forwards in front of him. To this movement, or to its continued repetition, the male responds by pursuit and mounting, the female halting as soon as she is clasped. Sometimes, especially in the proœstrous period, the receptive female responds to the male's attentions by wild running about the cage, and perhaps also by biting and kicking. Occasionally, too, the male does not mount before some minutes have passed, spending the intervening period in examining the female's body, his own body, or the wires of the cage. When, however, the copulatory act does appear, it "comes with such definiteness and orderly sequence of elements that it stands out in marked contrast and is never confused with this background of promiscuous activities."[338]

Attempts to analyse the effective stimulus evoking this series of separate acts that together make up the smooth and continuous performance of mating have yielded remarkable results. Stone found that rats that had been blinded long before puberty showed no diminution in their sexual excitement prior to their first mating. Their blindness does not delay the appearance of puberty, nor does it decrease their potency or ability to find the female in a cage. Since these blinded animals respond adequately to the movements of receptive females, it is evident, as Stone has declared, that visual stimuli are unnecessary for the perception of the characteristic movements of the œstrous female. But this experiment does not necessarily imply that vision is not normally used by the rat in finding its fellows.

Stone's [338, 343] experiments on rats and rabbits have

also shown that the sense of smell is not essential for the appearance of the sexual act in the pubertal male, and that it does not form an essential part of the sexual act of the adult. It is also doubtful whether the olfactory stimulus has any excitatory function in the inexperienced male. If the olfactory bulbs are destroyed before puberty, the appearance of the mating response is in no way retarded, nor is potency decreased. The only obvious effect of these experiments is that operated animals stop sniffing. Stone, however, considers that under normal conditions the olfactory receptors may be used, to some extent, in differentiating the sexes, and perhaps also as distance receptors for locating females. One is reminded of the fact that a house containing a bitch in heat will be surrounded by a ring of dogs throughout a night.

Since Stone found that a combination of blindness, loss of the sense of smell, loss of the sense of taste, and removal of the facial tactile vibrissæ in no way affected the sexual response of the male rat, he concluded that cutaneous and deep sensibility are the fundamental senses involved in stimulating mating behaviour. Observation showed that the amount of excitement aroused in a young male rat depended mainly on the excitability and responsiveness of the receptive female. Females that moved quickly when touched were most effective in stimulating sexual aggression. On the other hand, those that did not respond to the tactile stimuli of the male, but responded only to rough treatment, such as is adopted by the more aggressive adults, seldom stimulated strong sexual excitement. Non-aggressive adults behave in the same way as young males. By increasing the skin sensitivity of an unreceptive female, so that she responded by immediate retreat to the attentions of a vigorous young male, Stone was able to provide some evidence in favour of his view. This experiment was supported by another, in which a young female guinea-pig, whose movements corresponded very closely to those of a receptive female

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rat, was placed in a cage with a young male rat. The two showed no fear of each other, but the guinea-pig ran from the rat whenever he touched her. After she had repeatedly done so, the young male made strong attempts to mount. Stone's elaborate series of experiments led him to the conclusion that "in some way the movements of the female ordinarily supply the stimuli which under the proper conditions initiate the act of mating."

Avery's [30] researches into the reproductive behaviour of guinea-pigs support Stone's finding that the effective stimulus to mating behaviour does not operate through visual and olfactory receptors. His experiments add no support, however, to Stone's conclusion that the receptors of cutaneous and deep sensibility are the primary organs through which the mating stimuli become effective. Avery's view is that "there is a minimum of discrimination between receptive and non-receptive females and a maximum of trial and error mounting." If a male guinea-pig finds a receptive female in a colony and loses her, he finds her again only with difficulty. In his search for the receptive female he may try almost any female, until he again discovers the right one. Louttit [236] agrees with Avery's view, stating that "the behavior of the female is the determining factor in the discrimination." Avery has shown that destruction of the olfactory bulbs of the brains of young male guinea-pigs in no way retards the development of their sexual responses. There is no significant difference between them and normal males of the same age in regard to sexual aggressiveness and ability to beget young. He also showed that olfactory impulses are unnecessary for the maintenance of sexual activity, by performing the same operation on two adult males. Like Stone, Avery is careful to point out that these experiments show only that males deprived of their olfactory mechanisms can enter unhandicapped into sexual activity, as soon as post-operative shock has disappeared. They do not show

that olfactory stimuli are not normally used in the discrimination of receptive females, nor that olfactory stimuli, emanating from the œstrous female, do not normally aid in activating the sexual impulse.

It is perhaps dangerous to extend a generalization from rats, guinea-pigs, and rabbits to all lower mammals, and to declare that in all of them the activation of copulatory response may be independent of olfactory, and perhaps also of visual, stimuli. It is, however, fairly certain that such a declaration is more likely to be true than not. It is also possible that in all lower mammals the attitude of the female is, in some way or other, a necessary factor in eliciting the full sexual response of the male.

The problem of "abnormal œstrus" hinges on this possibility. Every female laboratory animal, except apparently the rabbit, allows the male to mount and copulate only when she is in œstrus. The only non-laboratory animals which are said to copulate outside oestrus are the llama and camel. According to keepers in zoological gardens, both of these animals will take the male at any time.

Analysis of abnormal œstrous behaviour involves the following considerations. Is the abnormal mating behaviour the same as that of true œstrus? Is the behaviour capable of explanation in physiological terms, or can it be explained only by reference to psychological concepts?

The results of Louttit's investigation of the behaviour of guinea-pigs throws some light on a possible difference between mating during true œstrus and mounting at other times. In his efforts to find receptive females, the male guinea-pig tries to mount every female he encounters. Actual copulation does not take place except at œstrus, when the female responds to the male's advances by assuming an adequate posture. At other times, though the male may succeed in mounting, he is very quickly thrown off by the female, and perhaps bitten. The unreceptive attitude of the non-œstrous

PLATE X

Tierpark Hellabrunn—München phot

IMMATURE MALE BABOONS IN THE MUNICH ZOOLOGICAL GARDENS

(See p 258)

female is enhanced during pregnancy, when she usually squeals protestingly even when touched. Now, though it is quite certain that actual mating does not occur except at œstrus, it is equally certain that mounting occurs at other times. One has to consider, therefore, whether many of the cases of "abnormal œstrus" that Heape had in mind were not really the abortive attempts of males to mount non-receptive females. Such behaviour is fairly common. Bulls are often reported to jump pregnant cows, and in so doing, cause abortion.

Sexual behaviour, though essentially part of a reproductive mechanism, is after all but a fraction of the total responses of an adult animal. The question therefore arises whether it is not possible that the mounting response, once it has appeared in an adult animal, soon loses its reproductive specificity. In the terminology employed by Pavlov this would imply that the sexual act emerges initially as an unconditioned response, when the animal is in a physiological state determined by the activity of the gonads. This unconditioned response having been executed a certain number of times can be evoked by conditioned, (previously neutral), stimuli which are associated in some way with the initial social situation.

Stone's [343, 344, 346] investigations into the effects on rabbits of the destruction of large areas of the cerebral cortex may throw some light on this question. The fact that removal of almost the whole cerebral cortex, as well as the olfactory bulbs, in no way influences sexual activity suggests that the neuro-muscular mechanisms involved in sexual responses are of a very low order, and, if anything, controlled mainly by subcortical centres. It is behaviour, however, that can be conditioned. Both Moss [267] and Louttit [238] have shown that mutual contacts can be inhibited by noxious stimuli, for example, electric shocks administered every time a male and female touch each other. It is conceivable, therefore, that the mounting behaviour

of male and female adult animals may lose its specificity, and be elicited in situations other than the adequate one of œstrus. It is perhaps possible that animals may respond sexually in all situations that contain any of the essential stimuli that are operative in a true œstrous mating. The guinea-pig proved an adequate stimulus to Stone's rat because of the peculiarity of its movements. Banta's [33] male wood frogs attempted to mate with anything moving—with one another, with bits of floating wood, with females as they sped along just beneath the surface of the water. Movement being the important element in the stimulus, a motionless female frog may float within a crowd of males without being molested. All these facts support a view that many obscure elements arising in their mutual relationships may stimulate animals to "abnormal" mounting. Such an explanation, ill-defined though it necessarily is from want of data, would satisfy the known facts. Mating behaviour exhibited at times other than œstrus becomes but part of a larger body of diffuse motor activities, elicited by subtle and obscure stimuli encountered by animals in the course of their daily life.

This explanation has emphasized the masculine element in abnormal œstrous behaviour, on the assumption that Heape, in defining the term, may have been partly considering the abortive attempts of males to mount non-receptive females. It is, however, possible that some female lower mammals, like the rabbit, are receptive at times other than true œstrus. The factors that would underlie this type of receptivity are obscure. Hammond has attempted to give an explanation in physiological terms of the "abnormal œstrous" activities of the pregnant rabbit.[137] He points out that the animal is always in œstrus provided conditions are favourable, suggesting that this is due to the fact that ripening follicles are always present in her ovaries. Large follicles can be found even in the luteal phases of pseudo-pregnancy and true pregnancy, except for a

period between the thirtieth and fortieth hours after the successful coitus that induces ovulation. During this period the does will not mate. This exceptional interval of ten hours, "the only time in the breeding season when large follicles are not present in the ovaries", is the period corresponding to the early stages in the formation of corpora lutea. Ovariectomy leads to the disappearance of sexual desire, and since the female will not receive the male except during phases of follicular growth, Hammond concludes that in the female rabbit "the desire for coitus depends on the presence of a mature follicle setting in action a nervous mechanism giving rise to the desire." This explanation is supported by Genther's experiments on guinea-pigs, but conflicts with the results of others, performed on rabbits and mice, which indicate that œstrus is not necessarily associated with the presence of ripe follicles.* Hammond himself, having shown that the "desire" of the cow in heat ceases before the tense follicles in her ovaries have ruptured, suggests that follicular tension is not the factor necessary for the stimulation of œstrous behaviour in the rabbit, but that the essential condition may be the "ovarian hormone". Since the ovarian hormone that is responsible for mating behaviour—œstrin—is not confined to the follicles, it seems difficult to prove that these structures are the primary agents in the evocation of sexual responses, normal or abnormal. Moreover in many pregnant mammals which do not mate, the placenta is a veritable storehouse of the hormone. Unless the rabbit reacts to œstrin in its overt behaviour in a way which is fundamentally different from the reaction of most mammals hitherto studied, it seems unlikely that "abnormal œstrus" in the pregnant rabbit is due to the physiological effects of the hormone. In spite of Hammond's explanation, the factors underlying the abnormal heterosexual behaviour of the rabbit still seem to be as obscure as those that

* See p. 119.

determine its known homosexual responses. Whether or not the two have equal significance remains to be seen.

The effects of the corpus luteum upon behaviour are mainly confined to the females themselves, and since a female in a luteal phase is neither receptive nor a stimulus to the mating response, the behaviour of the males is only indirectly affected. The luteal phase is essentially a phase concerned with maternal behaviour, so much so that one finds it difficult to avoid adopting a teleological point of view in describing it. All its effects seem designed to facilitate the care of the young that may be born. The factors underlying the maternal behaviour exhibited by an animal during the luteal phase are due to the chemical influence of the corpus luteum. These effects are the same during pregnancy and pseudo-pregnancy. The extent to which they are manifested in pseudo-pregnancy depends entirely upon the extent to which the corpora lutea become functional in a sterile œstrous cycle, and this varies in different species of mammals. In the unmated rat pseudo-pregnancy passes unnoticed. In the marsupial its duration is often the same as that of true pregnancy, and its effects upon behaviour are the same. Thus Hill and O'Donoghue [169] report that the marsupial cat cleans its pouch during pseudo-pregnancy, in the same way as it does during true pregnancy, even though its uterus does not contain young. This observation could be supported by many others of the same kind, all showing that the fundamental basis of maternal behaviour amongst mammals is the secretion of the corpus luteum.

Investigations into the muscular activity and food consumption of rats and guinea-pigs have yielded significant results bearing on the social stimulus to sexual activity. Slonaker,[327, 328] by means of automatic recording devices, has shown that rhythmical changes occur in the activity of mature female rats. These variations are not exhibited by ovariectomized adults

or females either before puberty or after the menopause. Males do not show comparable fluctuations unless they are confined in cages closely adjacent to those of active females. Sexually mature female rats show a distinct rhythmical increase in activity approximately every fourth day. This corresponds very closely with the periodicity of œstrus, the time when the female readily accepts the male, the cycles of activity synchronizing with the œstrous cycles. Cyclical changes in food consumption also run parallel to the œstrous cycle, the least intake occurring at œstrus during the maximum of muscular activity. Food consumption is not increased during pregnancy, but the average daily activity of females carrying young is less than two-fifths of that of non-pregnant females. There is a constant drop in activity following successful mating, the distance covered by the female the day after the mating being about a seventh of her performance on the previous day. Lactating rats are also less active than pregnant rats, but their food intake increases considerably, by amounts that are proportional to the growth and number of their young.

Slonaker's results correspond closely with those Kinder [213] obtained in her quantitative study of nest-building activities in the albino rat. It is well-known that all rats, male or female, begin to build nests from about their twentieth day—the time of weaning. This activity appears to develop relatively independently of learning. The extent to which it occurs varies with different environmental conditions. For example, rats build more during the cold than during the heat. At 80° Fahrenheit all animals stop building, with the exception of mothers suckling young. The nest-building activities of the sexually mature female show cyclical variations that synchronize with the œstrous cycle. The maximum amount of building occurs at the time of greatest food intake, and the minimum synchronizes with œstrus, the time of greatest muscular activity and least food intake. There is a very

great increase in building activities at the time of parturition and during lactation.

In her discussion of these facts, Kinder points out that nest-building is a thermo-regulative activity. It is increased at times when rats have to protect themselves against heat loss, for instance, at low temperatures during lactation. On the other hand, the least amount of food consumption and nest-building occurs during œstrus, when running activity is greatest and heat production is consequently increased. The two phases of greatest industry in nest-building, the luteal phase in the non-fertile cycle and the five days before parturition, do not appear to be periods in which there is any known necessity for heat conservation. These phases can, however, be correlated with events occurring in the ovaries, particularly with the development and retrogression of corpora lutea. Periods of nest-building industry are closely comparable with the pouch-cleaning performed by the pseudo-pregnant and pregnant marsupial cat. In the present state of our knowledge it is safe to conclude that the fluctuations in nest-building activity are the result of the interaction of external environmental factors and internal physiological ones. Probably since these fluctuations are exhibited only by sexually mature females, they are mainly dependent upon those factors that determine ovarian periodicity. The manner in which physiological events connected with the ovaries are translated into overt patterns of nest-building behaviour is as obscure as the manner in which the morphological changes characteristic of œstrus are related to œstrous behaviour.

Many of the facts described by Kinder have been confirmed by Sturman-Hulbe and Stone,[349] who have also shown that the wave of nest-building activity of the lactating rat can be prolonged by frequently replacing the more mature offspring by younger litters. This fact is of very great interest, because several observers have shown that this experimental procedure

does not prolong the normal diœstrous interval of lactation, which lasts about three weeks in the rat. Another significant observation they report is that a female may repeatedly pick up her own tail, carry it to the nest and deposit it there, if the nesting tendency is strong, and no materials are available. They also found that the normal mature animal, the female having her first litter, females that have been blinded, and those that have been deprived of their olfactory receptors, do not differ in the behaviour involved in nest-building, delivery, nursing, and the general care of their young. Sturman-Hulbe and Stone consider that external conditions are less effective in stimulating nest-building than are internal physiological conditions. In particular, they emphasize that the wave of nest-building industry occurs about the time of parturition, thus suggesting that it is activated by some internal factor. It remains to be seen whether or not this internal condition is a function of the formation of a corpus luteum immediately after parturition.

The physiological mechanisms underlying the process of lactation are still obscure. In some mammals, for example, the guinea-pig and cow, œstrous cycles continue during lactation. In others, such as the ferret and rabbit, an interval in which œstrus and ovulation do not occur follows parturition. (The duration of this "lactation interval", as it has been called, is fairly constant throughout a species.) The mouse and rat belong to the latter class but experience a post-partum œstrus and ovulation, which, if mating occurs, may result in a further pregnancy, and which, in any case, results in the formation of corpora lutea. In the absence of pregnancy, the post-partum corpora lutea become functional, but it is doubtful whether the suppression of the œstrous cycle for the lactation interval of three weeks is due to their activity. It is clearly unnecessary to consider that corpora lutea are the essential factors responsible for the suppression of œstrus during the lactation interval of the mouse and rat, since there are

many mammals whose ovaries do not contain corpora lutea during any part of the period of reproductive inactivity which they experience during lactation.

Numerous observers have shown that if a litter is removed from a lactating rat or mouse, the normal lactation interval of reproductive inactivity is soon ended by the appearance of œstrus. It has also been shown that though foster-mothering may prolong lactation considerably in the rat and mouse, it does not extend the quiescent interval of three weeks.[328] The fact that œstrous cycles soon restart when sucking is discontinued during the lactation interval indicates that the act of sucking is the primary stimulus in the mechanism of lactation. There is no need to assume that sucking is a nervous stimulus. It may simply maintain the flow of milk, and the cessation of milk secretion when suckling is discontinued may be due to the pressure exerted on the secretory cells of the mammary gland by the milk that accumulates in the ducts. Since the anterior part of the pituitary gland controls the ovarian cycle, it is clear that the suppression of œstrus during the lactation interval is an effect produced through the pituitary, which, in some way or other, reacts to the condition of the mammary glands. Were it not for the fact that foster-mothering does not appear to prolong the lactation interval in the mouse and rat, one would be inclined to suggest that the anterior lobe of the pituitary reacts to the metabolic condition of the nursing mother. The drain of nursing might affect her metabolism in such a way that the function of the pituitary would become affected.

The physiological events of the period of lactation have important effects upon behaviour. Animals that experience œstrous cycles during lactation will continue, while nursing their young, to manifest the same heterosexual responses as they display during œstrous cycles not complicated by nursing. Animals that have a lactation interval will not be receptive to the advances of males, nor will they stimulate those

advances, and their attentions will be almost entirely centred upon the care of their young.* The maternal responses of a nursing rat weaken as the period of weaning approaches. If young rats are removed from their nests and scattered over the floor of a cage, the mother generally replaces them almost immediately, but her efforts to do so become fewer when the experiment is repeated successively in later stages of the lactation interval.[349]

The manner in which the physiological condition of lactation translates itself into fixed overt patterns of behaviour, depending upon neuro-muscular mechanisms, is altogether obscure. Nursing behaviour does not appear to depend upon the activity of internal secretions, nor does it seem possible that it can be stimulated by a specific metabolic condition. On the other hand, the behaviour of many animals indicates that maternal responses are compounded of a group of unconditioned responses. Thus no significant difference is found between the behaviour of a primiparous and a multiparous rat.

In this chapter a brief outline has been given of the effects that œstrus, pseudo-pregnancy, pregnancy and lactation have upon the behaviour of the lower mammal. These phases of reproductive activity determine the main movements within a social group. Of particular importance is the fact that œstrus is the only time when the female of most species is receptive, though she may continue to prove a stimulus to the mounting responses of the male at other times. Œstrus forms the last part of the follicular phase, which is the normal sphere of activity of the follicular hormone, œstrin. It is unknown why the female is receptive during only part of the follicular phase. It seems that behaviour is affected only after œstrin has been acting

* Some observations of Slonaker's indicate that rats may occasionally experience œstrous symptoms during the lactation interval. Whether or not these œstrous symptoms, which Slonaker inferred from the activity of the animals, are accompanied by ovulation is unknown.

for some time and in increasing amounts. It is also possible that its effect may be added to by the activity of some other substance the nature of which is unknown. Whatever the cause may be, the fact that the female of the lower mammal mates only during a restricted period is the main feature distinguishing the social behaviour of the lower mammal from that of the monkey and ape.

CHAPTER IX

THE MENSTRUAL CYCLE AND BEHAVIOUR

IT was suggested in Chapter VII that the main difference between the menstrual cycle of the primate and the œstrous cycle of the lower mammal lies in the distribution of their respective follicular phases—phases during which the mating hormone, œstrin, is effective. The follicular phase of the lower mammal ends virtually with the cellular destruction that characterizes œstrus, and the endometrium of pseudo-pregnancy is built up, under the influence of luteal hormones, from an endometrium that has undergone degeneration at the time of ovulation. In the primate, on the other hand, the effects of the active secretion of œstrin are manifest throughout the cycle, although its main effects, as judged by the changes in the sexual skin, occur before ovulation. The growth of pseudo-pregnancy that follows ovulation is superimposed upon a persisting pro-œstrous endometrium. Interpreted in this way, the difference in sexual behaviour between primates and lower mammals reflects their different sexual physiological mechanisms. The matings of the lower mammal are confined to short œstrous periods, towards the end of the follicular phase. The matings of the primate, as is explained below, are diffused over the entire cycle, but vary in frequency according to the varying degrees of the activity of the follicular hormone.

The sexual skin is a controlling factor in the social behaviour of those species of monkeys and apes that exhibit cyclical external changes. Many incorrect interpretations of the activity of the sexual skin have been made in the past. In 1876 von Fischer [106] sug-

gested that the colour of the hinder parts of the female monkey renders her conspicuous to the male when viewed from afar. This suggestion was criticized in the same year by Darwin,[79] who gave as his opinion that, "as monkeys are such gregarious animals", he would have thought "that there was no need for the sexes to recognize each other at a distance." As an alternative view he suggested that it seemed "more probable that the bright colours . . . serve as a sexual ornament and attraction." Darwin did not differentiate between the cyclical coloration of the sexual skin of the female macaque and the bright coloration of the face and hindquarters of the mandrill. In his argument for sexual selection as a factor in evolution, both were considered to be ornamental characters, even though he admitted that Rhesus monkeys formed the only mammalian species known to him in which the female was more ornamental than the male. The coloured hinder parts of monkeys were grouped with their beautiful and varied coat colours as characters "acquired through sexual selection exclusively as ornaments." In Darwin's opinion, as "monkeys have the habit of turning their hinder ends towards other monkeys, it ceases to be at all surprising that it should have been this part of their bodies which has been more or less decorated."

It is now known, however, that the cyclical changes in the sexual skin of female monkeys and apes is caused by the hormone œstrin, and is part of the cycle of changes that involve all the reproductive organs. It belongs to an entirely different category from the permanent secondary sexual characters which in mammals are almost certainly not caused by that hormone. Pocock[287] in 1906, returning to von Fischer's view, considered that the swelling and reddening "serve as a source of information to the males" of the sex and condition of their fellows when seen at a distance. This suggestion incorrectly assumes that the sexes are normally segregated. Pocock also lends his support to Darwin's view

PLATE XI

Photograph by J. E Saunders

THE BIGAMOUS FAMILY PARTY OF MONKEY HILL

(In foreground. See p 144 and compare with plate XII)

that the coloration is an ornamental character. "It may be that the colour and inflammation appeal to the æsthetic sense and sexual emotions of the males and act as an aphrodisiac impelling them to pair with females in which the characters are pronounced rather than with those in which they are poorly developed or absent."

It is known that sub-human primates mate at all times, and it is generally believed, though incorrectly, that they experience nothing similar to the œstrus of the lower mammal. According to Corner,[72] for example, "the manifestations of sexual desire may be considered to be diffused over the entire reproductive cycle." This, too, is Allen's opinion,[9] while Hartman [142] writes that

> "as a general rule, the females (*rhesus macaques*) will accept the male whenever given the opportunity. We have at least a hundred observations on this point. Some females have, however, consistently refused the male, and certain ones have an antagonism to one or the other of our males, but the stage of the menstrual cycle has nothing to do with their refusal or acceptance."

In another paper Hartman [149] makes the generalization that "primates have no definite 'heat' periods, but copulate at any time, some species with great frequency." Miller,[258] too, attacking the view that monkeys experience periods of sexual heat, concluded from a close study of the very limited literature on the subject that both sexes of sub-human primates engage in sexual activity to an equal extent at all times. The evidence at his disposal was not strong enough to warrant the conclusion he drew. Miller inferred from Hamilton's [136] well-known paper, "Sexual Tendencies in Monkeys and Baboons," that female sub-human primates

> "were not subject to a psychological œstrous cycle, but were ready to accept the male at all times when not physically incapacitated (as by traumatism or recent parturition). The

males, far from having their sexual responses solely and automatically released by the female when in one definite and special physiological condition, or having their sexual interests fall into abeyance outside of a season of rut, were sexually attracted by any adolescent or adult female at any time."

This conclusion is inferred only from negative data, for Hamilton's paper contains no reference to œstrus or rut, and menstruation is mentioned only as a sign of sexual maturity. Miller also refers to Montané's [260] papers on the birth of a chimpanzee, writing that "the question of rut is not specifically alluded to but the female is represented as having been ready to respond to the sexual advances of the male" at any time. This again does not lend any support to a view that sub-human primates do not experience periods of increased sexual activity. Reference is also made to a paper by Kempf [211] that concerns the sexual activities of six Rhesus macaques, only one of which was a female. Kempf's observations are mostly on homosexuality. His paper contains no definite reference to œstrus in the female or to rut or periods of increased desire in the males. Miller also quotes Sokolowsky's [331] statements regarding a chimpanzee. Sokolowsky writes that a certain adult male chimpanzee "demanded repeated intercourse every day with his females. For this purpose he sprang down and seized one of the females who even if she struggled at first, had to yield finally to his superior strength." This is hardly justification for Miller's inference that "no periodical œstrus was apparent". In addition to Hartman's statement which has already been quoted, and two others which do not in any way add to his argument, Miller also cites two authorities, Köhler [217] and Gear,[123] whose opinions definitely conflict with his own conclusions. Köhler writes that an increase in sexual desire accompanies sexual-skin swelling in the chimpanzee, and that sexual desire is absent during the menstrual flow, while Gear states that a pronounced change occurs in the behaviour of baboons during the period of genital enlargement.

"The animals lose their restlessness and usually remain quiet in a corner of the cage, even ceasing to care for their fur. . . . In the females under observation, it was at this time that they permitted and even solicited the advances of the male, resulting in frequent acts of coitus."

Gear's statement Miller considers to be the only record he found suggesting "the occurrence of a period of rut in any primate". Actually, apart from those of Köhler and Gear, many observations have been recorded which conflict with the conclusion he drew, the evidence showing that monkeys and apes do experience heat periods.

Geoffroy Saint-Hilaire * observed that "female monkeys, although they receive the male frequently at all times, become very desirous when the external changes in the sexual skin are most conspicuous. Their 'heat' is most pronounced at the beginning and end of menstrual bleeding." This statement, while it associates the swelling of the sexual skin with an increase in the manifestations of sexual behaviour, is incorrect with regard to the time relationship between swelling and menstruation (see p. 86). Geoffroy Saint-Hilaire also noted that coitus is infrequent during pregnancy, when the cycle is suppressed. In their paper on the marmoset, Lucas, Hume, and Smith [240] note that the mating periods of this animal seem to be demarcated. They write, with reference to a particular female, that coitus was observed on March 23rd and during the next two or three days.

"Then attempts became fewer and less acceptable to the female, and finally ceased altogether. During the ensuing months there was no sign of œstrum, and when the young male was at liberty he paid no more attention to the female, through the bars of the cage, than he did to the other male."

Pocock described the pairing of baboons as occurring after the menstrual bleeding, that is, during the period of pudendal enlargement, and correlates the swelling

* Quoted by Breschet.[52]

in the female with "the extreme length of the intromittent organ in the male of Baboons". He did not note whether pairing also occurs during the quiescent period of the cycle. A period of heightened desire in the female chimpanzee is described by Fox,[116] who writes, regarding a pair living in the Philadelphia Zoological Gardens, that the sexual act is more frequent, more desired by the male, and more acceptable to the female during the period of perineal swelling. On the other hand, a pair of orangs in the same animal collection copulate daily without relation to the menstrual cycle. His observation on the chimpanzee is confirmed by Tinklepaugh,[358] who states that the female chimpanzee is receptive during only one half of the cycle. Spiegel gives as his opinion that although the common macaque may copulate at all times, excitement is most intense about the middle of the cycle, when sexual-skin activity is most pronounced.

My own observations both of captive animals in zoological gardens and of wild baboons in South Africa amply corroborate the view that monkeys experience periods of increased desire.

Monkeys and apes, as Darwin noted, have the habit of turning the hinder ends of their bodies towards their fellows. In captivity this behaviour is also directed to human beings and sometimes to domestic animals. The ultimate significance of this form of response, which may be termed *presenting*, is sexual. It may be exhibited by both male and female monkeys from a very early age in many apparently asexual situations, but at puberty, when the sexual skin first becomes active, presenting becomes a frequent act of obvious sexual purport. This change in the frequency and significance of the act of presenting can be observed at puberty in all monkeys and apes that show swelling of the sexual skin. From this time it may be a most insistent sexual response—at any rate in captivity—and as such it affords valuable evidence of the state of sexual excitement in any given animal.

From my own observations of captive primates it is evident that the extent to which they engage in sexual pursuits varies greatly among the individuals of a species and in different species. Adult female chimpanzees present and are sexually receptive mainly during the phase of pudendal enlargement. Gibbons, which do not show any sexual skin changes, have only rarely been seen to present to each other, and have never been observed to copulate. The same is true of langurs. Cercopitheque monkeys, which also do not show sexual-skin changes, are somewhat more active sexually, but very rarely mate in captivity. On a few occasions species of this genus have bred. Mangabeys, which show pronounced sexual-skin changes, always exhibit sexual behaviour, but mostly at the time of pudendal enlargement. During this phase, behaviour has almost continuous sexual reference. The females repeatedly present and continuously examine their ano-genital regions. If attempts are made to stroke a certain tame female of this genus, at present in the London Zoological Gardens, when her sexual skin is swollen, she always tries to bring her pudendum into contact with one's fingers. At the height of swelling her sexual excitement becomes intense. Its abatement is as dramatic as is the subsidence of swelling. Almost all macaques behave sexually. No periodicity has been noted in the rarely observed sexual response of bonnet monkeys and adult female kra monkeys (common macaques). Neither of these species show such pronounced changes in the sexual skin as do Rhesus macaques, which seem to mate more freely when the sexual skin is active than when it is quiescent. Adult pig-tailed monkeys show striking swelling of the sexual skin and mate at all times of the cycle, though most frequently during the stage of maximum perineal enlargement. The Moor monkey, which also shows a characteristic sexual-skin cycle, is again sexually most active during the phase of swelling.

Baboons show more pronounced changes in the

sexual skin than do other primates. During the phase of quiescence of the perineal region, caged specimens rarely, if at all, exhibit sexual interest. When coaxed to the wire of the cage they occasionally present, but more frequently their interest lies in having their fur "picked". During the phase of pudendal enlargement, however, they present insistently without encouragement. At this stage it is comparatively simple to take smears for investigating the cycle of cellular changes in the vagina without in any way restraining the animals. Observations of the habits of baboons living under relatively "natural conditions" in colonies, both in the London Zoological Gardens and in the Zoological Gardens at Munich, also indicate that the sexual activity of a female, and the extent to which she stimulates sexual behaviour in the male, vary directly with the amount of pudendal swelling she exhibits. The social unit in these colonies is the harem, which may include one or more females. In a "monogamous" family, the bond between a male and his female is closest at the time when her sexual skin is most swollen, and it is then, also, that they copulate most frequently. In a harem that contains more than one female, priority is almost always taken by the female "in œstrus". I have seldom seen a male overlord copulating with a female whose sexual skin was quiescent, if another female of his harem showed full sexual-skin swelling. The œstrous female usually spends the day sitting and moving in close contact with her overlord, while the quiescent females are always more active and may wander some distance away from the overlord. Thus at the time the photograph reproduced on Plate XI was taken, the two females of a harem were showing an equal degree of swelling of the sexual skin, and both were paying an equal amount of attention to their overlord. When the photograph of Plate XII was taken, the female of the same harem, who is seen grooming the overlord, had a swollen sexual skin, whereas the sexual skin of the female sitting some distance away was quiescent. During

pregnancy and the lactation interval, when their sexual skins are inactive, female baboons rarely exhibit sexual interest, and only on rare occasions have they been observed copulating with their males. Moreover, during these reproductive phases, they do not appear to activate the sexual responses of the males.

My observations of wild Chacma baboons in South Africa show that their social habits correspond closely with those of captive Hamadryas baboons living in colonies. In general, their behaviour agrees with the pattern of behaviour outlined above. It was noted in Chapter III that twelve adult females belonging to the same harem were shot on the same day on a farm near Grahamstown in the Eastern Province of the Union of South Africa. Eleven of these twelve females were either pregnant, lactating, or in different stages of the luteal phase of an infertile cycle and their sexual skins were inactive. Only one of these eleven showed signs of recent mating.* One female had a fully swollen sexual skin, and her vagina contained semen. This observation provides striking support for the view that the sexual-skin activity is closely correlated with sexual responses of adult baboons, and indicates clearly that captive conditions do not disorganize the essential elements of their sexual behaviour.

Analysis of the facts outlined above indicates that those primates which show pronounced cyclical changes in their sexual skins are more active sexually than those that do not. It might be argued that this is an effect of captivity. The observation made in South Africa conflicts with such a view. Moreover, all the monkeys in the London Gardens, except the baboons on Monkey Hill, are housed and fed in the same way, and this common environment cannot be said to approach the natural conditions of any one species more than of any other. It is true many species show a greater adaptability to captive conditions than do others, and that some species live only a short time in captivity. But conspicuous

* She had recently ovulated and spermatazoa were found in her uterus.

variation in the amount of sexual expression occurs in species which enjoy an equal longevity in captivity—for example baboons and Cercopitheque monkeys.[113] It is obvious from these considerations that speculations about the effects of captivity cannot obscure the correlation that exists between sexual activity and activity of the sexual skin.

Langley and Sherrington [225] have shown that the afferent fibres of the sexual skin of the Rhesus macaque enter the spinal cord by the sensory roots of those nerves whose motor roots supply the vagina. This fact suggests a possible explanation of the relation between sexual skin and sexual behaviour. It seems reasonable to surmise that when the sexual skin is swollen with œdema, its sensory nerve endings are stimulated by pressure and that this reflexly rouses the animal to sexual behaviour.

Generally, the lower mammalian female will mate only when she is in œstrus, which is a phase of behaviour that reflects a series of anatomical changes determined by the activity of œstrin. Œstrus synchronizes closely with ovulation, so that the effect of œstrin may be said to be the prevention of sterile mating. In the sub-human primate mating occurs most frequently when the follicular hormone, œstrin, is most active just before ovulation and swelling and coloration of the sexual skin are at their height. The biological significance of the activity of the sexual skin is therefore clear. Œstrin performs the same function in primates as in the lower mammal. Females gradually pass into an attractive condition, and remain in that state while they become desirous. After ovulation they revert into an unattractive and non-desirous state. In this way mating chiefly takes place when it is likely to be fruitful.

It is important to recognize, however, that the sexual behaviour of the primate is uninterrupted, reflecting the more or less continuous activity of the hormone œstrin. Female monkeys and apes do not periodically

experience the abrupt transition from a sexual to a non-sexual state that is undergone by the lower mammal. Both male and female primates are always sexually active to some extent, their heterosexual interests providing the bonds that hold them together in permanent bisexual associations. It is in this that primate society differs from the associations which may be formed by those lower mammals that breed at all times of the year. In these associations the link between the male and female is constantly broken and remade. Sexual bonds become obvious only at œstrous periods that are separated from each other by phases of pregnancy and nursing. The male lower mammal is not stimulated sexually by a pregnant or lactating female, whereas the primate may be. The primate family consists of male, female or females, and young, but the family of the lower mammal consists only of the female and her young.

The manner in which the sensori-motor mechanisms of the primates differ from those of the lower mammals is reflected in the way the male primate selects the female "in heat". The rat responds to the œstrous female primarily by its kinæsthetic appreciation of her peculiar movements. The guinea-pig finds the œstrous female through "trial and error" mounting. On the other hand, observations go to show that in many species the male primate perceives the œstrous female mainly through visual and tactile receptors. The important element in his discrimination is the sexual skin. Unfortunately the particular characters of the skin that activate masculine sexual responses have not yet been experimentally analysed.

A monkey's response to the presentation of one of its fellows is manifested by a series of characteristic actions. With rapid movements of his lips and tongue he inspects the proffered hindquarters, which he may sometimes examine with his snout and hands. If he proceeds to the final step in this pattern of behaviour, he mounts and copulates. The strongest stimulus to the

full display of this series of muscular activities is a female with a swollen sexual skin. The sexual bond between a male and a particular female when she is in this phase is their mutual sexual interest. The excited female presents repeatedly and the male almost invariably responds. It is only after he has copulated many times that he fails to react in some way or other to the sexual stimulus.

The attitude of the female monkey is a very important factor in stimulating the attentions and sexual responses of the male, but her presentation is not an essential factor in eliciting his sexual responses. One monkey will sexually examine the perineal area of another even though the latter has not presented. His interest may be manifested simply by an attitude of bodily attention with his eyes centred on the ano-genital region of the animal that has attracted him. His behaviour may stimulate a reciprocal sexual response and with much smacking of the lips the animals may engage in further sexual activity. This type of behaviour is commonly exhibited within a harem. The overlord's attention is caught by the perineal region of one of his females, usually when her sexual skin is swollen. He bends his head forward, his hand reaches out, his lips and tongue move and, having thus stimulated a sexual response in the female, he mounts and copulates.

It is difficult to determine by theoretical analysis whether the specific stimulus to sexual activity is the presentation of the hindquarters and their subsequent examination. It is necessary to distinguish here between perineal examination that occurs during grooming, and perineal examination that has only sexual significance. An observer will readily recognize the distinction between the two forms of investigation. He may occasionally notice grooming activity assuming a directly sexual character, and the opposite transition might also be observed. Clearly perineal examination in itself is not the essential stimulus to sexual responses, since it so frequently occurs unaccompanied by direct

sexual activity. In spite of these considerations there can be no doubt that the swollen perinæum of a female "in heat" is a stronger sexual stimulus than a quiescent sexual skin. Its examination is more extensive and prolonged, and the number of times it stimulates copulation is much greater than in the case of the quiescent sexual skin. Although experiment alone can decide, it seems probable that the visual stimulus of the colour and form of the sexual-skin swelling is an important factor determining mating responses. The facts of comparative neurology harmonize with such a view. Elliot Smith [96] has repeatedly emphasized the fact that the primate brain is a "visual" brain, that one may measure its evolution in a scale of increasing correlation between hand and eye movements. A blind monkey is a very awkward animal. Its actions are continually impeded by the obstacles it encounters. It does not respond adequately to the movements of its fellows.

The visual stimulus cannot, however, be the only factor underlying the overt sexual responses of monkeys and apes. Many primate species do not undergo any apparent changes in the sexual skin. In these species the specific stimulus to sexual response may possibly be some unknown physical cyclical change appreciable to members of the species. The attitude of the female might stimulate the male, as it does in the rat, or the male might find the female by trial and error, as the guinea-pig does. It is also conceivable that the females of those primate species that do not undergo external changes do not experience cyclical periods of increased sexual activity. In that case they would be fertilized by "chance" in the course of a series of "undetermined" matings.

Up to this point discussion has been focussed upon the possibility of a specific physiological stimulus activating sexual response in sub-human primates. It is, however, necessary to consider the further possibility of the particular characters of their reproductive mechanisms permitting a much greater degree of

conditioning of sexual responses than can occur in the lower mammal. In considering in the previous chapter the abnormal œstrous behaviour of the lower mammal, the suggestion was made that many elements associated in some way with initial sexual acts may become conditioned stimuli evoking sexual responses in apparently asexual situations. If this is possible in the lower mammal it is even more possible in the primate which experiences continuous physiological sexual activity. Actually many situations that do not seem to have any immediate sexual reference stimulate sexual responses in the sub-human primate. For example, a monkey may present itself sexually to a tormentor. A bitch in such a situation would run away. It is probable that the bitch does not behave sexually in such a situation for the reason that its peculiar physiology prevents it from being directly sexual except for two brief periods in the year. It is perhaps even more likely that the different behaviour of these two animals in the same situation is determined by their different kinds of intelligence—by the differences in their sensori-motor equipments. The greater complexity of the neuro-muscular mechanism of the primate allows its behaviour to be conditioned to an extent impossible in the case of an animal like the dog, whose limbs, unlike the monkey's, are not investigatory organs. The sexual responses of the sub-human primate can be linked to many situations which are not intrinsically sexual, but which, once the association is formed, change in character owing to the infusion of a sexual element. Its efficient sensori-motor apparatus and its peculiar reproductive physiology allow its sexual responses to extend beyond the narrow range of stimuli that serve to evoke these responses in lower mammals.

CHAPTER X

THE INDIVIDUAL WITHIN THE GROUP

REPRODUCTIVE mechanisms have so fixed and unvarying an influence upon the social life of the lower mammal, that the mutual reactions of the individuals in one breeding group are usually a counterpart of the social behaviour exhibited in another. The stable character of the groups reflects stereotyped social responses which are largely unlearned. The evidence shows that in a mammal such as the laboratory rat, sexual reactions are compounded of a series of innate or "unconditioned" responses.* They are a manifestation of its growth, and not of its learning. However, it is unlikely that sexual responses would remain altogether unconditioned in circumstances different from those of the laboratory. Moss has shown that a potent male rat will not cross a mildly electrified grid to reach an œstrous female, and her normal approach to the male may be similarly inhibited.[267] His experiments have been confirmed by Louttit, who, by simultaneously administering electric shocks every time male and female guinea-pigs touched each other, effectively modified the animals' normal social reactions. As he suggests, "contact behaviour can be entirely suppressed if the conditioning is continued long enough."[238]

Modification of sexual behaviour undoubtedly occurs amongst most wild mammals. A weaker animal does not try to obtain access to a female if a more dominant male is present. The suppression of its sexual approach may either result from the previous administration of "noxious stimuli" by the more dominant male, or conceivably the inhibition might be conditioned in some

* Stone,[339, 345] Louttit,[237] Avery.[30]

other more complex way. The inhibition might result from the mere perception of the bigger and more powerful animal, or it might be determined as a reaction to the perception of the dominant animal attacking and injuring another weak animal.

So far as is known, the modification of sexual behaviour that occurs amongst lower mammals involves the sexual act alone, and does not concern other forms of social response. The sexual act is either inhibited through the elimination of a weaker animal by a more dominant fellow, or it becomes freed from physiological control and is expressed as abnormal œstrous behaviour which, like sexual inhibition, does not implicate social situations other than the sexual act itself. The particular responses connected with mating are liberated at times other than true œstrus probably as an effect arising from the presentation of conditioned stimuli. The abnormal œstrous response seems to have no further significance. The sexual activity evoked by a conditioned stimulus is not adapted to or linked with other social situations and bodily attitudes. In this the lower mammal differs from the primate, which may be said to prostitute its sex by the introduction of sexual stimuli into situations which in themselves are inherently asexual. A monkey can divert the aggression of a fellow by presenting it with a sexual stimulus which proves stronger than the stimulus that activated pugnacious behaviour. As was explained in the previous chapter, this difference between primate and lower mammalian behaviour is partly a reflection of different mechanisms of reproduction. It is also partly a reflection of different mechanisms of co-ordination, since the extent to which innate forms of response become modified depends upon the complexity of the sensori-motor equipment of the animal—the efficiency of its organs of perception, the range of its muscular movements, and the nature of its brain.

There are obvious reasons why the conclusions drawn from experimental investigations into the sensory

and learning capacities of animals need to be considered in the discussion of social behaviour. They provide a measure for the amount of modification of sexual responses that might occur within a group. They also give some indication of the effect the behaviour of one animal in a group has upon its fellows. Indeed, in some ways, the problem of mimetic responses belongs more to animal sociology than to the subject matter of comparative psychology.

In the variety of their behaviour and the rapidity and extent of their learning, monkeys and apes rank above all other mammals hitherto studied. They owe this position to the greater complexity of their neuromuscular equipment. Elliot Smith has pointed out that the arboreal environment, in which all but a few existing primates live and in which the ancestors of the group became extinct, enhanced the biological significance of visual, tactile, acoustic, kinæsthetic, and motor functions. The phases in the evolution of the primates, an evolution culminating in man, may be read in the progressive development of those parts of the brain in which these functions are represented.[96]

Since the eyes of the lower mammal are usually set more to the sides than to the front of the head, each regards a different set of events, and the two visual fields overlap very little. A specially sensitive retinal area or macula is not developed, and each cerebral hemisphere is mainly concerned with the stimuli affecting the eye of the opposite side. On the other hand, the monkey is like man in these anatomical and physiological characters. The eyes are set to the front of the head, so that the two visual fields overlap greatly, the movements of the two eyes being automatically linked together so that both concentrate on the same object. Since a large proportion of the optic nerve fibres remain uncrossed, each cerebral hemisphere receives impressions made upon both retinæ. The stimuli presented by the central object in the field of vision converge in each eye upon a corresponding sen-

sitive retinal area or macula. "Only the monkeys, apes, and men among mammals have a macula and enjoy macular vision."[97]

The anatomical differences distinguishing the eyes of the primate from those of the lower mammal are reflected in differences in visual function. Primates are the only mammals capable of stereoscopic vision—the full appreciation of the third dimension in space. A lower mammal like the dog or rat is "insensitive to differences of detail in visual objects", although it is able to distinguish between degrees of brightness.[203] Indeed a normal dog may not "depend on vision in making many of his ordinary responses in the field".[206] The hypothesis suggested by Hunter in 1913 [190A] that animals below man "have only a more or less crude pattern vision" has not been disproved except in the case of the sub-human primate.* Johnson found that the visual acuity of the monkey "compares favorably with that of the human subject under similar conditions," and Yerkes and Yerkes,[395] summarizing the results of experimental investigations into the visual powers of monkeys, write that

> "visual processes and seeing in monkeys are more varied, complex, and highly developed than in any other mammal similarly studied, except chimpanzee and man. Perhaps the suggestion is justified that monkey differs visually from man rather in what it sees, the configuration of the object observed, than in number or variety of sense qualities and acuity of discrimination."

Monkeys and apes can discriminate between differences in form, size, and the distances between objects. It is doubtful, however, whether these abilities are always employed as they are by man. They were apparently little used by the monkey investigated by Kohts.[220]

* See, for example, Fields,[104, 105]; Valentine,[364]; Munn,[269]; Johnson,[201-206]; Cole and Long,[68]; Warden and Warner,[370]; De Haan,[83 etc.]; Kohts,[220]; Köhler.[217]

"In detecting the main points of hindrance as well as in finding the means of unlocking, the monkey is chiefly, if not exclusively, guided by kinæsthetic but not by visual perception. The motor reactions of the monkey the sooner result in the fulfilment of the object, i.e. release,—the more reduced the field of their application is, for actions which are developed in a narrow field exhibit greater progress in their variety, improvement and perseverance superior to that obtained in a vast field." . . . "So very restricted is the monkey's field of attention that he fails to distinguish devices located at no more than fifteen inches from the centre."

An even more striking difference between the visual powers of the lower mammal and those of the primate is shown by their respective responses to colour stimuli. So far as is known, lower mammals are colour-blind,* but primates react not only to differences in the brightness of light but also to differences in hue.† In this connection it is perhaps significant that monkeys are amongst the most highly coloured of all mammals.

Other modes of perception have not been studied as fully as the visual receptor system.‡ It has been shown, however, that Rhesus monkeys form "auditory associations with somewhat more rapidity than cats, and with considerable more facility than do raccoons under similar experimental conditions."[320] Established data on the comparative acuity of other sensory systems in mammals are not available, but anecdotal accounts indicate that sub-human primates are at least as efficient as the majority of land-dwelling and arboreal mammals in most sensory functions, except perhaps smell. Their hands are believed to be particularly sensitive instruments of touch.

An animal can add extensively to its experience only by actively bringing its receptor organs into contact with

* See, for example, Gregg, Jamison, Wilkie and Radinsky,[127] Warden and Warner,[370] De Voss and Ganson.[90]

† De Haan,[83] etc., Kohts,[219] Köhler,[217] Yerkes and Yerkes.[395]

‡ See, for example, Woodrow,[385, 386] Shepherd,[320] Hunter,[191] Morgulis,[265] Gregg and McPheeters.[126]

the environment in which it lives. Our interests would be more curtailed than they are if we did not constantly "prick up" our ears to hear, and "crane" our necks to see. But we are especially curious about the world in which we live. Some animals, for example pigs, show an extraordinary contentment with a very limited environment. Part of this limitation is no doubt imposed by their lack of hands, and by the fact that the snout is the only specialized organ of contact they possess. Apes and monkeys, on the other hand, rival us in the interest, at any rate the immediate interest, they show in their environment. They are the only other animals that have hands—which, as Watt [376A] wrote, "like the stereoscopic eye, can go round and through things, so almost isolating them from their surroundings." Kohts found that the Rhesus monkey very nearly equals us in the variety of minute movements which its fingers can make. The tactile perceptions of sub-human primates must indeed be extensive when it is considered that in addition to hands they also possess prehensile feet. With its manual organs of touch the monkey or ape investigates every object in its surroundings. Everything is picked up, examined, carried to the mouth and smelled. "Watch a monkey and you cannot enumerate the things he does, cannot discover the stimuli to which he reacts, cannot conceive the *raison d'etre* of his pursuits."

The wide gap that separates the sensory discrimination and investigatory activities of the primate from those of the lower mammal leads one to anticipate that they differ considerably in their respective learning processes. Accordingly, if questions of technique are disregarded, one would be prepared to agree with such conclusions as Thorndike drew from his studies of cats, dogs, and monkeys.[354] Thorndike's methods are now widely known. A hungry dog or cat is confined in a problem cage and to stimulate its efforts to escape food is placed near-by. In the course of the random movements the animal makes, it operates a catch that

opens a door and so secures the food. Every succeeding time it is deprived of its freedom, it escapes in the same way, and gradually the number of random movements decreases until finally the only movement it makes to secure freedom is the adequate one of working the catch. From experiments of this kind, Thorndike found that cats and dogs learn by trial and error, and by similar methods he discovered that monkeys learn in a different and characteristic manner. After spending some time in useless movement, the monkey may suddenly go through the necessary series of movements as though they were part of an already established and adequate habit. The learning of the monkey thus differs qualitatively from that of the lower mammal, since such a solution does not bear the stamp of chance that characterizes "trial and error". It also differs quantitatively, since it is superior to that of the cat or dog in the greater number of habits that can be formed, in the greater rapidity of their formation, and in their greater permanence.

Thorndike's conclusions about the learning processes of the monkey have been confirmed repeatedly.* But in spite of such claims as Pavlov's [285] that even in human beings "the different kinds of habits based on training, education and discipline of any sort are nothing but a long chain of conditioned reflexes," students of the subject have been obliged to introduce the concept of "insight behaviour" into their discussions, since the laws of the reflex have not been found wide enough to explain the responses of even sub-human primates in experimental situations.

Insight is an inference from the facts of observation, and therefore lends itself to fairly ready explanation. The necessary criterion of insight, according to Köhler, is "the appearance of a complete solution with reference to the whole lay-out of the field."[217] When an animal is faced by a new and stimulating situation, insight is

* For example, see Shepherd,[322]; Köhler,[217]; Kohts,[220]; Bingham.[41, 43]

manifested if the smooth continuous course of movements that effect the successful solution to the problem is abruptly separated from any random movements that may have preceded it, and if the successful responses cannot be readily resolved into a series of separated acts as can those of a chance solution. An example will make this clear. Köhler's ape Sultan was in a room in which a banana was fastened high above his reach. There was also a wooden box in the room. At first he made ineffectual jumps at the fruit. Then suddenly he went to the box, pushed it towards the banana, climbed on to it, and then jumped successfully at the fruit. Obviously much more is implied in the term "insight" than is indicated in the definition given above. Yerkes and Yerkes write: "Learning with insight implies the presence of ideational processes or their functional equivalents, ability to perceive relations, and perhaps also to analyze and synthesize mental objects."[395] For the moment, however, these further inferences can be disregarded.

Although it is well known that sub-human primates also learn by trial and error—for example, Kohts found that the monkey she studied "has not the slightest idea of the purport of his actions", and therefore was "unable to foresee their consequences" [220]—it has been generally believed until recently that they are the only mammals in whose actions insight is manifested. The distinction that Thorndike drew between the learning of the primate and that of the lower mammal seemed to be well corroborated by numerous experiments—for example, those of Drescher and Trendelenburg.[93] The insight of the ape and monkey was therefore accepted as a distinct psychological entity—something not only altogether different from the trial and error responses of the lower mammal but also showing characteristics distinctive of human behaviour. The recent work of Adams,[1] however, has cast doubt upon the statement that lower mammals learn entirely by chance through trial and error. Adams repeated Thorndike's original

experiments, and on the basis of his own results, criticizes Thorndike's technique as deficient, his description as inadequate and his interpretations as faulty. The conclusions that Adams himself drew from these experiments and from others that he devised are in striking conflict with the traditional view of animal learning. He maintains that cats may learn through "trial and error", by the "gradual elimination of useless movements". This manner of learning is more frequently exhibited when the animals are excited and inattentive. They may also learn through "insight" —by "looking over the situation", and, having by chance discovered the movable elements it contains, directly and smoothly going through the course of movements that brings success. Provided that the animal's attention remains fixed, the problem is then generally learnt in one or two trials.

In one sense these experiments and conclusions are revolutionary. "Insight" is no longer a specific possession of the primates. As Russell suggested even before Adams' experiments were published, it would be extremely rash to assert that insight will not be revealed by further observations on dogs or rats. "Unfortunately, some animals—for instance, elephants—may be extremely intelligent, but the practical difficulty and expense of experimentation with them is so great that we are not likely to know much about them for some time to come."[302]

The experiments in which monkeys and apes reveal their insight usually involve the use of instruments—sticks, ropes and boxes—and it has always been believed that the apes show more insight in the use of implements than do monkeys. Thus Yerkes and Yerkes write,

> "among the primate types appears increasing tendency to modify environment in the interest of welfare and comfort. One of the most impressive expressions of this tendency is the utilization of objects as tools. Search of the literature reveals complete lack of evidence of such behavior in Prosimiæ; indications that only the simplest forms of instrumentation appear in

monkeys; abundant proof of the phenomenon in a variety of forms in the anthropoid apes, as also in man. Manifestly, instrumentation becomes increasingly possible and important between lemur and man. Probably it is one of the best indicators of mental status. Assuredly it places the anthropoid apes next to man in ability to achieve adaptation through modification of environment, and at the same time it indicates a great gulf between monkey and ape." [395]

This view, however, conflicts with the results of a series of experiments on a capuchin monkey published this year by De Haan,[87A] and it appears that the adaptive intelligence of monkeys is not widely separated from that of apes. De Haan's experiments involved the use of a variety of instruments, including bottles, rakes and boxes, which the animal had to move in order to get fruit suspended well out of its reach. It is unnecessary to describe these experiments here. From De Haan's description they appear to have been as well controlled as the classical tests made by Köhler on chimpanzees. In comparing the achievements of his monkey with those of other individual sub-human primates whose records have been published, De Haan concludes that his capuchin monkey was not only more intelligent than the gibbon, the orang and the gorilla, but that she easily held her own with the chimpanzee. These conclusions are by no means startling. They were foreshadowed in descriptions published by Romanes in 1882.[298] As De Haan suggests, however, it is unsafe to generalize from his experiments and to infer that all capuchins are as intelligent as all chimpanzees. Nevertheless, even if the behaviour of most monkeys will on further experiment prove to be less intelligent than that of apes, it is still significant that individual variation is great enough to make a capuchin monkey so closely approximate to the most intelligent chimpanzees that have been studied.

As Adams' and De Haan's conclusions indicate, qualitative estimation of the learning capacities of animals in terms of "trial and error" and "insight" is

of doubtful value. There do not seem to be any logical means of differentiating quantitatively between the insight exhibited by the cat in dealing with one particular problem, and the insight demonstrated by the ape in its solution of another. It may well be that no significant variations will be found in the ways that different mammals solve problems, when full allowances is made for differences in their neuro-muscular mechanisms and for the differences in the problems set for them. The two concepts—"insight" and "trial and error"—are not mutually exclusive and do not signify differences correlative with increasing complexity in sensori-motor mechanism. Indeed, some *Gestalt* psychologists no longer seem to consider that the two types of learning are different in kind. Tolman, for example, writes that insight solutions "are ones in which the new adjustments come *without* overt behaviour, whereas . . . trial and error solutions are ones in which this change comes only *through* overt behavior." In spite, however, of this difference, "all learning may be said to involve the representation of the ends of acts at moments before their actual occurrence." "The higher the animal, the more it would seem that these representations can be played with and manipulated; the more the animal can mentally add and subtract the acts to produce new representations; the more, in short, he can achieve 'foresight' as opposed to mere trial and error solutions." [361]

If these views are correct, it should be possible to measure the extent to which different animals actually do perceive the "ends of acts at moments before their actual occurrence", and so to obtain some idea of their comparative intelligence. It should also be possible to explain how such processes occur, and how, to paraphrase Köhler,[218] the several states, wholes, attitudes of a total field, are experienced as depending upon, and determined by, one another. Moreover, if it is a fact that responses are determined in this manner, it should be possible to explain how animals obtain their "repre-

sentations" of the outcome of acts before they are made, how they come to be intelligently linked with their surroundings. It may well be that sub-human primates do experience imaginal processes, that they are capable of abstraction and generalization. But this possibility does not tell one how they come to behave with insight. To say that an animal learns with insight is to say little more than that it performs a new act or experiment as though it were already an established habit. Instead of showing how an animal learns to do a thing, the experiment shows that it can do the thing, that the reactions elicited by the situation are already part of its repertoire of responses. This is a very significant consideration. *Gestalt* psychologists themselves emphasize the importance of the influence that an animal's experience has upon its present behaviour. Adams, for example, points out that until they have once done so, cats cannot associate the pulling of a loop at the back of a box with the opening of a door in front, any more than human beings could. Again, in the description of his own lever experiments he remarks that until by chance the cats move a lever, they cannot know that it is movable ; but once the movement has been experienced, the lever will be used in future similar situations as a thing to be moved. Köhler also states that he takes it for granted that "every chimpanzee above a certain very low age" has had some experience of movable objects. "He will have seized a branch in play, scratched on the ground with it, and so on." [217] There can be little doubt that almost every experimental animal comes to a new problem with a wealth of previously acquired learning. The muscular responses elicited by the new situation have already been formed. The more highly organized the animal the greater will be the experience it brings to every new situation, and the more likely it will be that elements and relations in the new problem that it faces have been previously experienced. Thus one can explain Köhler's insistence that for insight to be displayed it is necessary for the

entire lay-out of a problem to be accessible to an animal. Hence also it is apparent why monkeys, with their greater experience of the external world, show more of this insight behaviour than do cats and dogs. It is obvious therefore that if one is really to learn how animals adapt themselves to new elements in an expanding environment, for example to experimental situations, it is necessary to know how they have become adapted to all elements in their environment. The sort of animal one would have to observe in order to learn exactly how a chimpanzee reacts to the single situation of "a banana out of reach and a stick near-by" does not exist. It would have to be an animal that had been brought up from birth alone and without food in an empty grey room. The chimpanzees one can observe already know how to solve the problem.

Russell has suggested that

> "all animals that have been carefully observed have behaved so as to confirm the philosophy in which the observer believed before his observations began. Nay, more, they have all displayed the national characteristics of the observer. Animals studied by Americans rush about frantically, with an incredible display of hustle and pep, and at last achieve the desired result by chance. Animals observed by Germans sit still and think, and at last evolve the solution out of their inner consciousness." [302]

To-day this remark perhaps loses some force, since many American psychologists now join with Köhler in formulating their interpretations of animal behaviour in terms of *Gestalt*. It is perhaps more likely that the present situation of doubt and conflict arises from the fact that the problems of animal behaviour which psychologists are attempting to solve are too complicated for our present methods of research.

At the moment it does not seem that students of behaviour can provide any statistical measure of the comparative learning capacities of mammals. Indeed it is a moot point whether their conclusions greatly amplify a superficial impression of the gap separating

the behaviour of the ape and monkey from that of the lower mammal. Disregarding the manner of his statement, Thorndike's conclusions about the complex behaviour of sub-human primates are well supported by the results that most investigators have obtained in their researches into these problems. "Delayed-reaction" experiments have shown that memory, however it may be determined physiologically, is far better developed in the primate than in the lower mammal,* and other experiments have also clearly indicated that monkeys and apes are superior to other animals in their adaptive behaviour. All this may be simply due to the primate's possession of hands that are facile in movement, of eyes that can see the details of things, and of a brain that is complex in its structure. Endowed in this manner its experience of the external world is immensely greater than that of the lower mammal. In the language of Hobhouse,

> "what distinguishes the ideas of monkeys from those of other animals in so far as experiments like mine can measure them, is an increase in elaboration and articulateness. By increased elaboration, I mean that in experiments of this kind, the monkey is less the slave of the perceptual order. There is more work of the mind in the plans which he lays on the basis of his experience. And this is principally shown in the increased articulateness of the plan itself. The monkey can apply one object to another; that is why he can use a stick, a stool, a poker. It may be said, so could the dog, if he had a hand. I am not prepared to deny this hypothetical statement; but I would rejoin that if the dog had a hand, his intelligence would be developed in a different way." [177]

One might extend this speculation. If a dog also had a monkey's eyes and a monkey's brain, it would be a monkey and would behave like one.

The layman believes that monkeys and apes are very good imitators—by which he usually means that they reflect the actions of individuals they may observe. In actual fact it is uncertain whether they do imitate in

* Tinklepaugh, [356]; Yerkes and Yerkes, [394]; Köhler, [217].

this manner, or indeed whether they are better mimics than dogs. Thorndike [354] found that monkeys never learned to do things either by imitating him, by imitating other monkeys, or by being put through a task. Watson's experience was similar,[373] while Kohts, who investigated a monkey's ability to work locks and bolts, states that

> "the widely spread opinion respecting the greatly developed imitative faculty of monkeys seems greatly exaggerated. Demonstrative unlocking of the device by the experimenter does not teach the monkey anything, but only stimulates him in the performance of his task and shows him a definite spot where some kind of work is to be fulfilled." [220]

She found that the monkey upon which she was experimenting never displayed

> "exact imitation of specimen procedure . . . Imitative powers do not come to the rescue even when they would seem to have the best chance to be exercised, namely when actions which under the circumstances are by all means worth duplication, insistently arise before his eyes."

However, some workers hold an opposite view. Hobhouse, for example, maintains that not only monkeys and apes, but even dogs exhibit mimetic responses, while Yerkes and Yerkes are equally insistent that sub-human primates are exceptionally well-gifted in their imitative powers.

Such diversity of opinion demands explanation. There must be good reason if certain authorities abandon a belief in the existence of a type of behaviour that has given rise to so widely recognized a term as *aping*. The possibility that mimetic responses occur is, moreover, of primary importance in the consideration of the social behaviour of sub-human primates, since they are so well endowed with the sensori-motor equipment necessary for extensive adaptation of behaviour. Living as they do in permanent social relationships, they are provided with numerous opportunities for modifying their behaviour through imitation.

It is difficult to provide an adequate explanation of what is usually meant by a mimetic response. As Adams has written, "imitation is a slippery category with which to deal." The layman believes that one animal simply copies the actions of either a fellow or a human being, or behaves as if it were doing so. It is advisable, therefore, to examine more closely the nature of such activities as would be superficially termed "imitative".

If a monkey has the opportunity he will examine one's clothes, put his hands in the pockets, pull at shoe-laces. Throw a monkey a parasol or a stocking and he will play with these objects as if he were imitating the actions of human beings. Actually it would be surprising if the animal did not pull on the stocking or open the parasol, since these are objects made to be manipulated by hands—and monkeys have hands and, what the handed prosimiæ lack, macular vision to guide their manipulations. Many seemingly imitative activities of sub-human primates are thus manifestations of their investigatory activities, and do not necessarily involve any element of imitation.

Some other forms of social behaviour are often termed mimetic, although they too may not imply active imitation. These activities are mainly those in which individuals of a group respond similarly to the same stimulus—for example, the flight of a troop of baboons as a result of a warning bark given by one of its members. Another possible example of this kind of behaviour was given at the beginning of this chapter. It was suggested that an animal's sexual activities might be inhibited by its perception of a more dominant animal attacking and injuring another member of the herd to which it belonged. Watson states that social responses of this kind are congenital and that they do not involve the process of learning, the examples he cites being drinking, peering into cracks and holes, and warning cries. He points out that "care is not always taken in these illustrations to ensure against the possi-

PLATE XIII

Photograph by J. E. Saunders

A MONOGAMOUS PAIR OF BABOONS ON MONKEY HILL
with an attached bachelor on their left (See p. 225)

[*face p.* 166

bility of response to a common stimulus, i.e., the stimulus which may have set off the response in the first animal may also have acted upon the other members of the group." However, he adds "there seem to be genuine cases, though, where the stimulus acts upon one animal, inducing an instinctive mode of behavior which in turn, becomes the common stimulus causing group activity." [375]

Watson adequately defines genuine imitation as a "*relatively instantaneous regrouping of old habits.* It is presupposed that all elements (unit habits) are present and that the stimulus (pattern, act to be imitated or copied) leads to a response which, from the observer's standpoint, is like the pattern." This definition clearly applies to those social responses of children in which one—usually prefacing his act with the remark, "I can do that too"—copies some unusual stance assumed by another. It is necessary to consider whether it also applies to such seemingly imitative responses of monkeys and apes as are not included in the types of reaction discussed in the preceding two paragraphs, and whether there is any real justification for the statement made by Yerkes and Yerkes that the chimpanzee "frequently exhibits imitative responses".[395] These authors write that the imitation of the chimpanzee ranges

> "from the apparently compulsional interest in and observation of the behavior of another companion, either human or anthropoid, to definite repetition of the essential aspects and relations of behavioral means to a certain recognized and desired objective. We recognize, and we believe any competent observer can demonstrate, in the average to superior chimpanzee, intelligent forms of imitative behavior. Imitation, as we hope we have made abundantly clear, is not a form of behavioral adaptation, but instead a condition of response."

In spite of their hope it is difficult to recognize precisely what these authors mean in this context by the phrases "a form of behavioral adaptation", and "a con-

dition of response". It is important to know whether or not the so-called imitative behaviour about which they write is the same phenomenon defined by Watson. It would also be of interest to know whether it is ever possible to establish that one animal repeats, in order to obtain some desired objective, "the essential aspects and relations" of behaviour which it may have observed. In other words, it is necessary to decide from the point of view of "economy of hypothesis" whether the available facts about so-called imitative behaviour of apes and monkeys cannot be explained, without reference to mimetic responses, by other and better established theories of animal learning. The descriptions given by Haggerty in his well-known paper provide an excellent basis for the consideration of this question.[135]

Haggerty defines four levels of imitative behaviour. At the lowest level a monkey's attention is arrested by moving objects, especially by the movements of its fellows. At the next level, the monkey responds to the actions of a fellow by moving after it. To neither of these types of response does Haggerty apply the term *imitation*. The lowest level of social response to which he does apply the term he exemplifies as follows:

> "one animal performs an act, gets food in a given locality and goes away. Another animal which observes its behavior goes immediately after to that locality as if to get food. What the second animal does in that locality seems at this level of behavior to have no relation to the behavior of the first animal." . . . "More clearly entitled to be called imitation is that behavior in which the animal responds to an imitatee, not only by going to a definite locality, but by attacking a particular object. . . . The most perfect type of imitation is exact repetition in detail of the act of the imitatee."

Haggerty's own interpretations are implied in the descriptions that he gives. Like Yerkes and Yerkes he believes that true imitation, as defined by Watson, is displayed in the activities of monkeys. The levels of imitative responses that he postulates may be considered in turn.

The interest shown by monkeys in the movements of their fellows is an obvious outcome of their social lives. So far as the individual animal is concerned the exhibition of such interest is essential in group life, since he enjoys only such social and material advantages as he is able to withhold from his fellows. For this reason a monkey usually reacts in some degree to every movement of neighbouring animals. Like all animals, monkeys are more readily stimulated by moving than by stationary objects. Certain anatomical considerations lead one to suggest a possible morphological basis for this type of response. Elliot Smith has advanced the view that in the primate, investigatory reflexes are mainly built up of linked eye and hand movements. He has emphasized the importance of proprioceptive impulses from the eye muscles to the brain, which establish connections with other neuromuscular mechanisms. It is thus conceivable that an animal's body reacts quite mechanically in response to movements of the eye. Such responses could not, of course, be claimed as mimetic.

It is questionable whether or not the third and fourth types of social response defined by Haggerty are, as he considers, truly mimetic. The evidence for his view is ambiguous. The activities of a monkey manipulating an object recently handled by a fellow do not afford the data for an observer to decide whether the animal is imitating behaviour it may have perceived, or whether it is simply inquisitively investigating an object that has been made a significant element in its environment by the activities of a fellow animal. Moreover, when a monkey performs a series of acts in a manner that accurately reflects the recently exhibited behaviour of a fellow animal, it is not necessarily copying a series of movements that has been displayed. It may be simply responding to a common stimulus independently, but in such a way that it accurately simulates the behaviour of another monkey.

In order to demonstrate imitative powers in animals,

comparative psychologists usually show an animal how to do an act, or allow a trained animal to perform before an untrained fellow. According to Watson, such methods actually only serve to localize and enhance the intensity of the stimulus, a view that is supported by Washburn [372] and by Kohts, who states that the performance of an act in front of a monkey only points out the area in which it must apply its activities. Adams considers it important to add that the enhancement is not in the stimulus, "but in the organism and is properly regarded psychologically as amplification of perception, accrual of meaning or enhancement of context." [1] Watson criticizes the experimental basis from which Haggerty drew his conclusions. In these experiments monkeys that had failed to solve a mechanical problem after a considerable number of trials, succeeded when the act had been performed before them by a trained animal. Watson points out that in allowing animals a hundred chances of learning "by imitation", sufficient opportunity is provided for the animal to learn spontaneously. "With an animal as agile and as varied in his interests as the monkey, it is never possible to tell when a burst of activity will lead to the solution of the problem by the perseverance method." He adds that it is possible to assume that the only effect of the act of the "imitatee" is to set off two congenital forms of response on the part of the imitator. "The one was the following instinct,—i.e., to go to the place where a group of monkeys had just been and to peer into the same holes that other monkeys had just peered into, etc.; and the other the tendency to attack moving objects first." After these two "factors of imitation" have operated, the animal learns of its own accord.[375]

These considerations seem to indicate that no facts are available to prove the view, maintained by Yerkes and Yerkes, that the chimpanzee imitates by definitely repeating the essentials of a form of behaviour carried out by another animal, for a recognizable and desired objective. On the other hand, so far as the data allow

of generalization, they indicate that "imitation" within a social group of animals consists essentially in the continuous modification of one animal's environment by the activities of the others. In this way, imitation is a form of "behavioral adaptation". The behaviour of one monkey modifies the behaviour of another by constantly introducing into its immediate environment elements and relations that were previously unnoticed. Its response to these may be identical with the previous response of another monkey, since the same kind of animal is responding to the same situation. Imitation, implying social modification of behaviour, may thus mean no more than that the experience of one monkey or ape within a group may be shared by all its fellows.

CHAPTER XI

APES AND MONKEYS IN THE WILD: GENERAL

IN defining a theory of mammalian sociology earlier in this book, it was suggested that social behaviour —the interrelation of individuals within a group—can be theoretically regarded as an end product of the interaction of ecological factors, the mechanisms of reproduction, and the psychological variations of individuals. Up to this point the development of this theme has been analytical in nature. The subjects discussed have been the physiological and sociological aspects of reproductive mechanisms, and individual and so-called mimetic behaviour. A significant conclusion has emerged from these considerations. Much less variation occurs in reproductive mechanisms and in intelligence among apes and monkeys than one would expect from a superficial survey of the problems. In other words, monkeys and apes show great similarity in the most important determinants of the overt expressions of social behaviour. They are also influenced by the same ecological factors. All species are mainly frugivorous, and, with the exception of the baboons, drills and mandrills, they are forest dwellers. With so much in common it is therefore not surprising to find that the social life of all sub-human Old World primates seems to be built upon the same plan. In spite of the fact that a gorilla may be fifty times heavier than a monkey—a difference in weight far greater than that existing between an average new-born baby and an average adult man—there are no significant variations in the more conspicuous manifestations of their social lives.

Indeed the social habits of different monkeys and

apes appear to be so similar, that naturalistic accounts of their lives in the wild soon acquire a distressing monotony. In paraphrasing these accounts in this chapter, the claims of accurate description have made a certain amount of repetition unavoidable,* since it has been found necessary to consider each family and genus in turn. The social behaviour of wild baboons is considered separately in the following chapter.

The romantic glamour that has surrounded the gorilla ever since Du Chaillu [94] returned to Europe in the middle of the nineteenth century, is probably responsible for the fact that there are numerous accounts of the habits of this animal, even though it is in some ways the rarest and least accessible of all primates. Du Chaillu wove a fantasy about an enormous manlike monster of the forest, that tore up trees, bent guns, stole native women, and lived in huts high above the ground. It is only within recent years, however, that fairly accurate records, more or less free from emotional bias, have been published.

The gorilla is found in the forests of the western parts of Central Africa (Gaboon and Cameroons), and in the mountainous regions around Lake Kivu, north of Lake Tanganyika. It is unknown whether or not the western form, *G. gorilla*, interbreeds with the more powerful eastern form *G. beringei*.† Both species are mainly terrestrial, although they are confined entirely to the forest zone.

Gorillas are usually met with in small bands which

* No attempt has been made to cite all the authorities upon whose accounts my statements are founded. In searching through the literature I have tried so far as is possible to read original descriptions rather than accounts based upon them, such as are found in natural history works, e.g. Brehm's Tierleben.[176] Lengthy bibliographies can be found in the latter books, in handbooks on the primates, and in such sociological works as Briffault's *The Mothers*.[53] Almost all the available information about the behaviour of apes has recently been discussed by Yerkes and Yerkes in their book *The Great Apes*.[395]

† Schwarz [308] describes a new form of gorilla from the Ituri forest, *G. gorilla rex-pygmæorum*.

vary in size from four to about fifty individuals (Burbridge [57] describes "scores" in one troop). Adult males are often found wandering alone. According to Reichenow,[292] the western gorilla lives in smaller parties than does the eastern species. Small bands are reported to include as a rule only one adult male, but several males may be found in larger troops. These herds are said to be formed by the temporary association of smaller family parties, but it is obviously difficult to decide how much confidence should be placed in travellers' interpretations of the facts. It is probably safe to assume that a single adult male who is met with several females in his party, is polygynous. On the other hand, it may be wrong to assume that a party of several adult females and only two adult males consists of two families. It is as likely that the second male has no mating relationship with the females, and that he is admitted into the family party subject to the assured dominance of the first. Such a social group is fairly common among baboons, whose social habits have been more closely observed than those of other sub-human primates.

Most observers state that the gorilla is "fiercely" polygynous, but Reichenow and Von Koppenfels [221] maintain that it is monogamous. Reichenow bases his opinion mainly upon his observations of the sleeping nests of gorillas, which, with only one exception, he found either singly or in pairs. Each nest accommodates only a single animal. Describing a pair of adult nests, he writes :

> "The whole family is limited to these two nests. If a third or, exceptionally, a fourth nest is present, these are *much smaller* and belong to half-grown youngsters. Therefore we can draw the important conclusion that the gorilla is not polygamous, but lives monogamously, and that the sexes do not unite only during the rutting time, but remain together for several years. The half-grown animals continue apparently for a long time in the company of their elders, perhaps even until they found families of their own." *

* Quoted from the English translation in Yerkes and Yerkes.[395]

Reichenow's explanation of the exceptional case in which he found seven nests together clearly indicates his strong bias in favour of the view that the gorilla is monogamous.

> "Of these four belonged to grown and three to young animals. Obviously here two families had made their night camp together. That it might be a male gorilla with three wives seems to me improbable. If polygamy existed with the gorilla then we would oftener find three nests of grown animals in a family group." *

Reichenow does not attempt to explain why some adult male gorillas wander in solitude.

Barns,[35] Burbridge,[57] Akeley,[20] Jenks,[196] Chorley,[64] Dyce Sharpe,[316] to mention only a few field workers, disagree with Reichenow's opinion that the gorilla is monogamous, and hold that it is polygynous. In Uganda, Chorley recently observed a family of mountain gorillas consisting of an adult male, four adult females and two young ones. "The old grey-backed male seemed to have a surly temper, for sometimes he would grab one of his wives by the head and succeed in throwing her ten yards away. Nevertheless, his wives appeared to regard him with real affection, and drove away two males that came too near."

There is no logical reason for assuming, as some naturalists appear to do, that reports of the polygyny of some gorillas conflict with accounts of the monogamy of others. The existence of lone adult males, the fact that almost all reports indicate a preponderance of females in bands, and the fact that the bodies of gorillas that are obtained by hunters often show clear evidence of fierce fighting, are consistent with the possibility that family groups are formed and maintained by virtue of the dominance of their male overlords.

Most observers maintain that gorilla bands scatter over a fairly wide tract of country during the day, to reassemble in the evening. This statement is not

* From Yerkes and Yerkes.[395]

strictly accurate, since the largest party that has been described was encountered at three o'clock in the afternoon.[57] In the present state of our knowledge definite conclusions about the banding of gorillas cannot be drawn. It seems clear that they live in harems, which may exist separately or which may sometimes join to form larger groups. No adequate explanation has been suggested for these temporary associations. It is possible that several smaller parties meet in an area rich in food, and it is also conceivable that certain parts of the forest provide better conditions for nest-building than do others. Burbridge describes a party that apparently came together to execute "what seemed a sort of crazy war dance".

There is a prevalent belief that each group of gorillas "owns" a tract of country which it forages early in the morning and late in the day in search of the young shoots that form its main diet. Thus according to Dyce Sharpe, the family party of the western gorilla, usually consisting of one adult male, four to six adult females with young, and perhaps one immature male, always patrols the same area of from twenty to forty square miles. Yerkes and Yerkes[395] sum up the question of the feeding habits of these animals as follows :

> "The gorilla is primarily a ground-feeding herbivore, which eats enormous quantities of plants and their fruits. It is extremely careless and wasteful of foodstuffs and therefore is compelled to wander over a considerable area. Partial to berries and other fruits which grow on bushes and trees, it climbs as necessary to obtain them. But certainly in case of the mountain varieties, and probably also the lowland forms, the bulk of the food consists of the tender portions of low-growing plants."

As evening approaches the gorilla settles down for the night and builds its nest. Accurate observation of its nesting habits have cast doubt on the validity of the delightful story that male gorillas sleep at the foot of a tree to protect their mates and young who have nested in its branches. These observations, however,

have shown that great variations occur in methods of nest building, which, according to Yerkes and Yerkes, can possibly be correlated with specific zoological characteristics, with local environmental conditions and with the seasons. Ground nests are commonest in the Cameroons and the Kivu, but in the Gaboon a large number of nests are also found in the trees. The nests, which are very crudely formed by pulling branches and twigs together, are not occupied for more than one night.

The chimpanzee is found throughout the forests of Central Africa, and, like the gorilla, is mainly frugivorous, living upon young shoots and fruits. Reports about its social life are very conflicting. It is said to live either in single family groups or in bands larger than those of the gorilla. Garner [122] observed chimpanzees in parties of eleven, five, three, and two, and almost all observers have reported meeting with solitary males. Yerkes and Yerkes, [395] after consideration of the literature of the subject, conclude that Garner was correct in his assumption that the chimpanzee is polygynous. Buck * gives a good description of a family group consisting of an adult male, two mature females, one of whom was nursing, and about eight immature animals, that had arrived at its camping-place for the night. He describes their behaviour when foraging, relating how the adults cuffed the too playful young animals. When they climbed into a tree to sleep, the overlord accompanied the female who was not nursing, and the mother ape disappeared "into the dusk".

According to Christy,[65] the chimpanzee builds a new sleeping nest high in the trees every night. Aschemeier [29a] came across three chimpanzees preparing a bed in the trees, and obtained the impression that one of them, a male whom he later shot, was not doing any of the work, but that it was "bossing the job." He does not record the sexes of the other two.

* Quoted from Yerkes and Yerkes. [395]

Little is known about the constitution or about the movements of the large troops that are sometimes encountered. Garner [120] has left lively accounts of "carnivals" held by bands of chimpanzees. A drum is built of clay, superimposed upon

> "a kind of peat bed, which, being very porous, acts as a resonance cavity, and intensifies the sound. . . . After the drum is quite dry, the chimpanzees assemble by night in great numbers, and the carnival begins. One or two will beat violently on this dry clay, while others jump up and down in a wild and grotesque manner. . . . the festivities continue in this fashion for hours."

Although this account obtains a certain amount of support from the reports of other travellers, it certainly needs scientific confirmation before it is accepted.

Sokolowsky's [331] account of sexual life in a chimpanzee harem is by far the best that has hitherto appeared. The harem he observed was a captive troop consisting of a few young females and a young male, who were dominated by an old male. The dominant animal

> "kept himself aloof up at the top of the cage, seated on a board, observing and controlling the doings of the others. If a quarrel arose he sprang down from his seat, and made an end to it by blows and bites. He never indulged in games or sports, but preserved his austerity which was respected by the others. The sexual appetite of this male was very interesting to note. He was very exacting in this respect, and demanded repeated intercourse every day with his females. For this purpose he sprang down, and seized one of the females who even if she struggled at first had to yield finally to his superior strength, and submit to copulation. When he saw the young male attempt intercourse with the females, he sprang on the couple, and drove the young male off with bites and blows. The young male succeeded in effecting intercourse only when he waited until the old male was asleep, and then made advances to the females who acceded. From my observation the old male exercised his power and strength in a despotic manner, and demanded sexually implicit submission."

The orang utan, which lives almost entirely in the trees, is usually found in the swampy forests near the coast and along the rivers of Borneo and Sumatra. Very little is known of the habits of the wild orang. Shelford,[319] who made a special effort to discover if it was polygynous, decided that the task was impossible "unless men can acquire arboreal habits".

The orang appears to be the least sociable of the apes, as it apparently never congregates in groups larger than a family party. De Crespigny[75] found orangs living in parties containing one adult male, one adult female and young, but notes that the male does not occupy the same tree as the rest of his family. If the latter observation is true, it is probably responsible for the view, stated by Schlegel and Müller,* that the male lives apart from the females except during a rutting season. For reasons given in an earlier chapter, it seems very unlikely that the orang has a rutting season, and Schlegel and Müller's interpretation of the animal's social habits, even though supported by that of Wallace,[367] cannot be considered conclusive. Deschamps † suggests that the orang lives in small scattered groups because of the scarcity of food. It is well known that the animal migrates for some months of the year into the depths of the forest when fruit is scarce elsewhere. According to Hornaday,[184] the males fight fiercely. Evidence of severe bodily mutilation suggests strongly that the social life of the orang has its basis in the harem, which is maintained by the dominance of its overlord.

Gibbons live in the Malay Peninsula, Southern China and in the Malay Archipelago. At least four species are recognized. Some authorities classify the siamang in a genus by itself, separating it from the genus that includes all the other gibbons. All are strictly arboreal, living in forests usually well above sea level.

Except for the hoolock and siamang, which live in large troops, gibbons are found usually in small family

* Quoted from Yerkes and Yerkes.[395] † *Ibid.*

parties. Sometimes old males are discovered living alone. Tickell[355] came across the Lar gibbon in parties of from eight to twenty individuals of all ages. "It is rare", he writes, "to see a solitary one; occasionally, however, an old male will stay apart from the flock." Yerkes and Yerkes[395] quote extensively from the posthumous notes of Spaeth, who had devoted "some months to an intensive study of the problems of reproduction in the gibbons of Siam." Spaeth found that the gibbons live for the most part in family groups, but early one morning he met with a band of males alone in a tree, concluding "that it was some sort of bachelors' club gathering". Yerkes and Yerkes also record some interesting observations made by Ogilvie on the social behaviour of gibbons. One of four adult gibbons which this observer had kept in his compound for six years bred, and "a black gibbon who was obviously the father attached himself to her, and the other two were chased from their accustomed trees and never allowed in the compound."

There is no definite evidence about the mating habits of gibbons, and statements that have been made on this subject are speculative. For example, Kloss reports that he did not meet Malayan gibbons in independent parties containing more than five individuals.[216] He adds:

> "The statement that gibbons are monogamous is one that I thoroughly agree with: whether however they divorce each other and take new partners from time to time we have yet to learn. The point is interesting, since such an able reasoner as Westermarck has come to the conclusion that the marriages of mankind are an inheritance from some ape-like progenitor."

The evidence for this statement does not appear to be embodied in the observations which Kloss records.

Gibbons are reported to call loudly to each other from sunrise till about nine o'clock, and then again towards evening. During the day they systematically work a particular area of the forest for food. There is no evidence that they build nests at night as do the

bigger apes. According to Candler,[62] a young hoolock, if caught and not tied or restrained in any way, will settle down to a solitary life in the compound in which it has been placed. The calls of the wild hoolocks "do not tempt him to revert to his natural life as a member of a wandering community." Other reports suggest that if the wild gibbons got hold of the captive animal they would tear it to pieces.

The langur monkeys of the genus *Pithecus* are scattered widely throughout India, Ceylon, Tibet and the countries on the east of the Bay of Bengal, as well as throughout the Malay Peninsula, Cochin China and Siam, and in many of the islands of the Eastern Archipelago, including Borneo, Sumatra and Java. The greater number of these species live in small parties of not more than thirty individuals, but some, like the entellus, live in large hordes.

Flower [110] reports that the dusky langur (*P. obscurus*) lives in Kedah, usually in parties of from one to six; the biggest he ever saw contained from ten to twenty animals. The white langur (*P. senex*) of Ceylon lives, according to Kelaart,[210] in parties of from three to four. Collett [69] provides a good description of Thomas's langur (*P. thomasi*) that lives in North-East Sumatra. It is strictly arboreal, never descending to the ground, and lives in troops which appear to consist chiefly of full-grown animals of both sexes. He once saw a party foraging in company with siamangs. Ridley [295] writes that the banded langur (*P. femoralis*) lives a strictly arboreal life in Tenasserim in small flocks of from six to seven, though it may also be seen singly or in pairs. According to Hose,[186A] the same monkey lives in the low country of Borneo, often near the sea-board, in parties of from ten to thirty individuals. Hornaday [184] states that the black langur (*P. johni*) is found in India usually in troops of five to ten members. Barbes' langur (*P. barbei*) lives in Tenasserim in somewhat larger parties of from thirty to fifty members. Banks [32] writes that the species *P. rubi-*

cunda, *P. cruciger*, and *P. chrysomelas* live in Borneo usually in "troops of six to ten individuals, solitary red or black ones it is true being very occasionally seen."

The Entellus langur (*P. entellus*) thriving under the protection it receives as one of the sacred animals of the Hindus—it is one of the monkeys of the famous Hanuman temples—is found in enormous and uncountable hordes in many parts of India. Blanford [46] writes that these monkeys are

> "commonly seen on the roofs of houses. They frequently pilfer food from the grain-dealers' shops, whilst the damage they inflict on gardens and fields renders them so great a nuisance that the inhabitants of the country, although they will not as a rule kill the monkeys themselves, sometimes beg the Europeans to shoot the intruders."

Away from villages, the Entellus lives either in the high trees of the forest or sometimes in rocky hills, in moderately large troops composed of males and females of all ages, and in single family parties. Occasionally old males are found wandering alone. MacMaster [255] has left a record of a small colony of Entellus monkeys "under the command, very strictly enforced, of a very fine male", which, judging from MacMaster's description, was the only adult male of the group.

In spite of excellent opportunities for observation of this species in temples and villages, very little is known of its social habits. On the authority of an article appearing in a Bengal sporting magazine, Jerdon [198] relates that the males "live apart from the females, who have only one or two old males with each colony". At certain seasons the adult males fight, and the vanquished join with bands of young unattached males. Blyth [47] reported that in one locality he found troops of males of all ages, and in another parties consisting chiefly of females. This observation is qualified by Hutton,[192] who states that

> "the males and females are promiscuously intermixed; and although quarrels will sometimes occur, yet as a general rule the

whole community lives together in peacefulness. With the Himalayan species the custom is the same, the males and females remaining together at all seasons, even when the females have young ones at the breast, or are followed by yearlings. The only approach to a separation at any season consists in the males of a troop keeping together and the females doing the same if there are very young ones among them; but the two divisions form but one troop; and I am not even yet quite sure that such a trifling division really takes place."

Another observer [190] records an interesting account of langurs fighting for females. He reports that he saw a group of males attacking a party of females that was in the possession of a single overlord. Some of the attackers were running along the ground, and others were making their way through the branches. While the three leading males of the latter party were pursuing the overlord, other males rushed into the herd of females and made off with them in small parties into the neighbouring trees. The recorder of this observation suggests that when the three leading males disposed of the overlord, they would have returned to the harem, and having forcibly evicted the males who had seduced the females, fought amongst themselves until in the end one big male was in charge of the entire female herd.

Although these observations clearly do not allow of any definite generalization about the social relationships of langurs, they suggest that the animal has a strong tendency towards polygyny. This inference is further supported, indirectly, by the numerous statements about the occurrence of lone males. It would appear that some langurs live in small parties consisting of a single harem, and that others, like the Entellus, band together to form large hordes consisting of numerous family parties. The internal stability of such organizations will, of course, depend upon the interaction of the dominant characteristics of the respective overlords.

The langurs resemble the proboscis monkeys * of Borneo and the guerezas † of tropical Africa in many anatomical characters; formerly the three types were classified together in a sub-family of their own. The proboscis monkey is often found in company with the crested langur in forests near water. It is usually seen in small parties, but both Lenz [231] and Hornaday [184] describe groups containing as many as thirty to forty animals. One small troop of thirteen observed by Hornaday contained several males; he does not state whether they were all adult. During the day groups of proboscis monkeys roam quietly in search of the leaves which form their main food, swimming those rivers across which they cannot swing. The guerezas live in parties of about the same size. Some species feed mainly on lichen, but Morley,[266] who wrote a report on the extermination of species of Colobus monkeys by fur traders, states that they also consume large numbers of insects.

The monkeys of the genus *Cercopithecus* are widely dispersed over the whole of Africa, and are classified into a larger number of species than are the members of any other primate genus. Most species have beautifully-coloured coats, for which they are extensively hunted. They feed chiefly upon fruits and leaves, often raiding plantations, and live in the trees, either in small parties or in large troops. Occasionally old males are found alone. Most observers maintain that both family parties and larger troops have leaders.

Blanford [45] encountered Grivet monkeys ‡ in Abyssinia in flocks of from twenty to thirty. Flower [109] saw them in parties of five or six individuals. The green monkey § of West Africa is found either alone or in small troops, while Burnett's monkey ‖ is reported to live in troops of about fifty individuals. Wroughton [352] notes that Stuhlmann's monkey (*C. leucampyx stuhlmanni*) is common near the Ruwenzori, where the forest and

* *Nasalis larvatus.* † Genus *Colobus.* ‡ *Cercopithecus æthiops.*
§ *C. sabæus.* ‖ *C. burnetti.*

bamboo zones meet. When foraging in search of young shoots, it does not stray far from the edge of the forest—or it would be killed by leopards. Loveridge [239] found that Sykes' monkeys were plentiful at Morogoro in East Africa. They are never seen in large companies, and individuals may be found alone. He also records that he caught a single toothless old male of this species, feeding in a native's maize plot. Other monkeys belonging to sub-species of the species *Albogularis* are said to live either in very large troops or in small family parties. Thus the Mozambique monkey is found either in large troops, which pillage gardens, or in smaller parties.

The Samango monkey * is encountered in the forests of eastern South Africa. In May, 1930, I collected three males, one of which was immature, the other two being nearly adult, in the Pirie Forest near King Williamstown. One of the older animals was found alone, the other two belonged to a party of twenty-five individuals whose sexes I was unable to distinguish on account of the thickness of the foliage. I frequently heard monkeys chattering in the trees, and in one place very near where the Samangos were seen, I came across a party of seven Vervet monkeys. † One of these was crying as a monkey does when it submits to punishment or some other form of domination.

The habitat of the Vervet monkey extends widely from East Africa to the southern extremity of South Africa. Loveridge [239] encountered "large companies" near Morogoro in East Africa, and states that "parties of them would descend on the cultivated plots in the early morning, placing one of their number in a tree to act as scout and warn them of the approach of any potential emney." Stevenson-Hamilton [337] declares that this monkey is found in the dry low country of Eastern Transvaal in small family parties, in pairs, or singly, but that farther south it lives in troops of at least forty. Grant ‡ also states that he has occasionally

* *C. samango.* † *C. pygerythrus.* ‡ Quoted from Elliot.[99]

observed a pair with their young. Sclater[312] notes that solitary males are often found. Fitzsimons'[107] account of the life of this monkey is by far the most lengthy that has yet been published. He writes that Vervets associate in troops of about a dozen to a hundred individuals of both sexes and all ages, in the forest belts of the eastern side of South Africa, along the wooded banks of the larger rivers and in patches of dense bush in various inland districts. Adult males frequently fight, the most dominant one assuming the leadership of the troop, while the vanquished become the solitary males that are often encountered. Although they usually subsist on the fruit of the forest, these monkeys often leave their arboreal homes to pillage orchards and plantations, sentinels being posted while the raid is in progress. The farmer suffers greatly from the depredations of these animals, since they destroy much more than they can eat, but he also gains from their activities since they help to keep down a variety of insect pests, including locusts. Fitzsimons records that he saw Vervet monkeys drop down from the trees on to the backs of antelopes, whose fur they proceeded to groom. The monkeys sleep clustered together in the branches of trees, and sometimes in sheltered situations on rocky ledges. On one occasion Fitzsimons encountered a score or more perched on the roof of the huge nest of a hammerkop bird. He also states that he has never yet "met two large troops of monkeys in the same locality. They seem to have their districts as carefully marked out as is the case with us."

The mangabeys of Eastern and Western Africa form a small group of monkeys that are larger and more powerful than the Cercopitheques. Little is known of their manner of life beyond the fact that they are mainly arboreal and frugivorous, and live in troops in the forests. The crested mangabey is found near the coast in parties of from five to six. Pechuel-Loesche *

* Quoted from Brehm.[176]

declares that the grey-cheeked mangabey is found either in pairs or in parties of three, and that old males may live alone.

The macaques, a group of arboreal and terrestrial monkeys, are found throughout India, whence they extend into Tibet, Northern China, and the Malay Peninsula. They are also found in Sumatra, Java and Borneo, and the neighbouring islands, as well as in Northern Africa, where lives the solitary African macaque, the Barbary "ape."

According to Jerdon,[198] the lion-tailed macaque (*M. silenus*) inhabits the dense forest near the Malabar coast of India, living in herds of from twelve to more than twenty. The Formosan, or round-faced macaque (*M. cyclopis*), inhabits the rocks and cliffs near the coast of the Island of Formosa. It takes to the forest only when food is scarce on the grassy hills by the sea. Swinhoe[350] records that it assembles in parties towards the evening, and that it feeds on berries, grasshoppers, crustacea, and tender shoots—sometimes raiding the fields of sugar-cane. The same author writes that the females of this species may frequently be seen in June in the hills, with young ones at the breast.

The Rhesus, or Bengal macaque, is found throughout Northern India and as far south as Bombay, living in hordes in the jungle, low forest, and rocky hills, and feeding mainly on fruits, leaves and insects. Muir[268] once observed a terrestrial party of Rhesus monkeys swimming to take to the trees. The Rhesus is one of the sacred animals of the Hindus, and numerous accounts have been given of the troops that are kept in a temple of Hanuman, the monkey god of Benares. According to Elliot,[99] "their numbers increased so greatly at one time in this temple that the government was obliged to interfere, and as their destruction would have been resented by the natives, a compromise was effected, and all but about 200 were carried into the jungle and set free." In spite of the excellent opportunity afforded for observation of this

monkey in a wild state, practically nothing is known of its social behaviour. Sterndale[336] relates that he once tried to get a baby Rhesus from a herd containing many nursing animals, and that he was turned on by the old males of the troop. The Rhesus has often been kept in large numbers in the London Zoological Gardens. My own observations, which are recorded in a later chapter, indicate that its social life is based upon the principle of dominance.*

The Hainan macaque is considered by some authorities to be a Rhesus monkey that has been introduced into the Island of Hainan; on the other hand, Elliot[99] considers it to be a distinct species. Swinhoe[350] relates that it is very common in the jungles in the south of the Island. On landing from a ship he encountered on the beach a large party, which at once retreated into a grove above the high-water mark. Swinhoe also records a quaint Chinese myth "that the Monkey has no stomach, but digests its food by jumping about."

The pig-tailed macaque lives in large companies in the jungles of the Malay Peninsula, Southern Burma, Banka, Sumatra, Java and Borneo, feeding principally upon fruits and seeds. Shelford[319] encountered this monkey in Borneo in droves led by a big male, and sometimes he found males living alone. The monkey is used by the Malays and Batakas of Sumatra to pick coco-nuts, the price of a trained animal being very high. The pig-tailed monkeys that live on the Island of Singapore are believed to be escaped captives.

The common or crab-eating macaque (*M. irus*) has much the same distribution as the pig-tailed monkey, and lives in troops that may contain as many as twenty individuals of both sexes and all ages. At high tides they remain in the branches of the trees, "but at low-water they take to the mud and hunt about for food, presumably for crabs."[99] Shelford,[319] who supports the latter observation, states that their chief enemy is

* See Chapter XV.

the crocodile. Ridley[295] maintains that this monkey "will not admit strangers into the family troop without a fight." He describes a fight between a party of these monkeys and six langurs for the possession of a ranbutan tree. Chasen[63] states that the monkey is now becoming scarce in Singapore. "A large isolated flock lives in the Botanic Gardens under conditions which are daily becoming more artificial. Adult males seem to be unusually numerous in this colony."

The Barbary macaques, found in Morocco, Algeria, and on the Rock of Gibraltar, live in trees or rocks, feeding mainly on fruit and leaves. They are said to be numerous in the forests of Barbary and to pillage the cultivated fields of the Moors. Both Sclater,[311] and an anonymous writer to the *Field*,[133] have given an account of the Gibraltar apes, which authorities believe were introduced from the African coast. In 1880 there were twenty-five in the troop, which was led by a large male. Sclater was told that when the monkey population numbered one hundred and thirty, at the beginning of this century, it was split up into several parties, one of which included thirty individuals. These smaller parties consisted of "an old patriarch, accompanied by several females and young ones of different sizes." Parties of males were also encountered. According to "C. H.", the anonymous contributor to the *Field*, the monkey population of the Rock was reduced to three in 1863, but fresh importations were made to keep the numbers up. Two or three introduced in 1872 were killed by the older inhabitants. In 1875, the troop consisted of six mature females, several young and two males, one of whom was the overlord. When the two males died, the troop was much given to squabbling. A young male born in 1874 was the leader of the troop in 1880.

As in the case of the langur, these observations of macaques are not sufficiently definite to allow one to draw firm conclusions, but they clearly suggest that the societies of these monkeys are based upon the

harem system—a system in which every adult male attempts to secure for himself as many females as possible—and that several family parties may unite to form large troops.

The rare Celebes "apes"* are found only in the island from which they take their name and in one or two of the neighbouring islands. They live in the trees of the forest either in pairs or in small bands of about eight animals, which, according to Hickson,[168] "invariably consist of a pair of adults and a number of young ones."

Accounts of New World primates indicate that their social systems are similar to those of the Old World apes and monkeys which have already been discussed. For that reason—and in spite of the fact that no data have been available for the consideration of their reproductive mechanisms—certain reports concerning their behaviour in the wild will be briefly referred to in the remaining pages of this chapter.

The douroucoulis (genus *Aotes*) are small nocturnal animals that in appearance little resemble monkeys. They are strictly arboreal and frugivorous and are found in the forests of South America—"from Nicaragua to the Amazon and Eastern Peru". According to Rengger[293] they usually live in pairs, but Bates[37] met them in "colonies". Allen[17] observed a family consisting of a male and a female with two young. The titis (genus *Callicebus*) are small and mainly diurnal, arboreal monkeys that live either in small bands of about six individuals, in pairs, or alone. Allen states that he collected an adult pair of Mount Duida "marmosets", and that the male was carrying a younger one of the same sex, probably its own infant. Field-reports about the sakis (genera *Pithecia* and *Chiroptes*), the uakaris (genus *Cacajao*), and the marmosets and tamarins of the Family *Hapalidæ*, indicate that these monkeys live in parties of about the same size as those of the douroucoulis and titis. Allen tells of a troop

* *Cynopithecus*.

of from fifteen to twenty uakaris which returned daily to the same tree to feed.

The small squirrel monkeys (genus *Saimiri*) are found in the valley of the Amazon, usually in large troops. Schomburgh * observed parties of more than a hundred individuals moving on the fringe of the forests. One of two males belonging to a party of twelve that were shot by Allen was carrying two young.

Squirrel monkeys have been reported to mingle with bands of capuchins, the New World monkeys that are most commonly exhibited in captivity. These monkeys are encountered either in small parties of about twelve individuals, in which females are said to outnumber the males, or in fairly large troops, which are said to have leaders. Such troops sometimes pillage cultivated fields. Solitary males are also seen, and Allen met with a single nursing female Azara capuchin, a species that is usually found in pairs or in small troops. Male capuchins, unlike the marmoset and howler monkeys, do not look after their young.

Capuchins have also been seen to mix with spider monkeys (genus *Ateles*), animals which are widely distributed in the forests of the northern part of South America. Bartlett [36] reports that the black-faced spider monkey travels in parties of from thirty to forty individuals, and Forbes [115] states that the red-faced spider monkey lives in troops that may number as many as one hundred. Other species of this genus, for example the variegated, Geoffroy's and the long-haired spider monkeys, are found usually in parties of from nine to twenty. Many observers note that males may be found living alone, and Schomburgh states that young can be seen in every troop.

The woolly monkeys live mainly in the forests of Brazil in parties of as many as fourteen. Bartlett [36] states that the brown woolly monkey is seen usually in pairs, and that sometimes four to six pairs live in the same tree. These monkeys also mingle with

* Quoted from Brehm.[176]

other species, and Bates[37] writes that they pillage plantations.

The well-known howler monkeys (genus *Alouatta*) of the forests of the northern half of South America are usually found in small parties, in which the females greatly outnumber the males. The Caraya howler was found by Allen[17] either in pairs or in small troops of from four to seven individuals, and according to this observer a troop of red howlers contains only a single adult male. Hensel,* who encountered howler monkeys in parties of five to ten, and who provides evidence that this monkey breeds at all times of the year, declares that each group is confined to a small fixed area of the forest. He also suggests that each party has a leader who controls the actions of any other adult males who may happen to be in the same group. Brehm quotes several elaborate accounts of "concerts" held by howler monkeys in the forest. The view first suggested by Humboldt that a number of monkeys partake in these "concerts" was qualified by Wallace, who maintains that all the noise is made by a single fully-grown male.

* Quoted from Brehm.[176]

CHAPTER XII

BABOONS IN SOUTH AFRICA

IF the Rev. W. Bingley[44] were still alive he would find many farmers echoing his opinion that baboons are "as tall as men, have sunken eyes, and are otherwise extremely disgusting," for since his time their reputation as agents of destruction has increased considerably. They are reputed to tear open the stomachs of young lambs to obtain curdled milk, and are condemned for the damage that they do to cultivated farm lands. A series of amazing legends has sprung up about their pillaging expeditions. They are said to post sentinels, and to conduct their raids in a manner suggesting preconceived planning of so high an order that the farmers' counter-attacks have to be very subtly arranged. One alleged method of dealing with baboons takes advantage of a belief that they cannot count above three, and proceeds as follows. When a troop of baboons is laying waste to an orchard, four men approach and frighten them away. If the four men then leave the orchard, the baboons will return immediately. If, however, two men leave and two remain hidden in the trees, the animals do not return. But since baboons cannot distinguish between three and four, one man remains hiding in the orchard and, when the animals foolishly return, proceeds to destroy them. Many tales like this, and others reminiscent of those already quoted in the first chapter of this book, are reported in Fitzsimons' work, *The Natural History of South Africa*.[107]

Apart from their depredations there are other facts that make baboons, drills, and mandrills in some ways the most noteworthy of sub-human primates. They are the largest of the monkeys, and are even more

terrestrial than the apes, rarely being found in the forest zone, and usually living in hilly, open country. They also seem to be the most gregarious of the sub-human primates. Forbes [115] states that Dr. Slack met the Doguera baboon of Abyssinia in troops of one to two thousand individuals. All known baboon species appear to have the same social habits, living sometimes in family parties, but more usually in large hordes.

The Hamadryas baboon, the Thoth of the ancient Egyptians, is found in the rocky ravines of the Sudan, Abyssinia and Arabia, in parties that may include as many as three hundred monkeys of all ages. The old males are always conspicuous in these troops, and are reported to take the lead when the party is on the move. Some also keep to the rear, and others move on the outskirts. Blanford [45] has recorded his impression of these baboons; he writes:

> "a troop collected on a rocky crag presents a most singular appearance. . . . On such occasions every jutting rock, every little stone more prominent than the rest, was occupied by a patriarch of the herd, who sat, with the gravity and watchfulness befitting his grizzled hair. . . . Around, the females were mainly occupied in taking care of the young, the smaller Monkeys amusing themselves by gambolling about. Occasionally, if a young Monkey became too noisy or interfered with the repose of one of his seniors, he 'caught it' in the most unmistakable style and was dismissed, with many cuffs, a wiser if not a better Monkey."

The Hamadryas baboon, which subsists mainly on roots and the fruits of low bushes, is seldom found near trees in Abyssinia, but farther south, near the Kilimanjaro, it is usually met with close to native plantations on the edge of the forests, in parties of from fourteen to twenty individuals. Like all other baboons, the Hamadryas very often pillages native gardens. It is said to wage constant war with the Gelada that lives in Southern Abyssinia. Both animals are reputed to be very ferocious and pugnacious, to post sentinels when they plunder fields, and to roll stones. Forbes states that it

is a common habit of Gelada baboons "to roll down stones from the rocky cliffs amid which they live, upon any approaching animal—the Arabian baboon being an especial object of their animosity." Both species, too, like all other baboons, are reputed to have a special series of modulated cries and grunts, "to warn, to indicate safety or false alarm, or to direct the general movements or conduct of the troop." From Von Heuglin's * account, it appears that the dusky Gelada dwells either in the open plains or in inaccessible rocky cliffs, in herds consisting of from twenty to thirty females and young, led by four to six old males. On rare occasions these parties unite with one another.

Yellow baboons live on rocky hills and sometimes in trees, in parties that usually consist of from fourteen to twenty individuals of both sexes and of all ages. This species preys extensively on farms, and has been seen to forage in company with bushbuck and wild pigs. Loveridge [239] tells of a yellow baboon that stopped in its flight to return and carry away a severely wounded fellow; of a female that snatched up a young baboon whose mother had been killed; and of a party of these animals attacking and killing a native child. Two incidents similar to the last are recorded by Northcote.[278]

The Chacma, perhaps the largest of all baboons, is found over a wide area in Africa south of the Limpopo River. It lives either on rocky faces that overlook ravines and valleys, or in the small outcrops of rock that are met with on the lower hills. Its food consists mainly of roots, the fruits of the prickly pear, the meally cobs and fruit it plunders from cultivated lands and also, it is believed, of scorpions and insects. It is a gregarious animal and lives in parties that may number as many as several hundred animals—Fitzsimons [107] mentions a horde of five hundred. Usually, however, a troop, which generally contains more adult females than it does adult males, numbers less than one hundred. Holub †

* Quoted from Elliot.[99] † Quoted from Forbes.[115]

has described one such troop as follows: "There were mothers taking care of their little ones; there were half-grown animals, the boys and girls of the company; but there did not seem to be more than three or four full-grown males." Many observers have encountered solitary males.

In the early part of 1930, I visited South Africa to collect anatomical material and to make observations of the behaviour of wild baboons. During my visit I also tried to obtain information about the damage these animals do to farm-lands. It seems that in some districts their depredations are considerable, yet in many places no steps are taken to prevent their ravages. For example, one fruit farmer, living in the Western Province, told me that a troop of from sixty to one hundred animals regularly pillages his orchards, particularly during the apple season, the animals approaching to within a hundred feet of his house. They are not frightened away by shouting and often enter his fields even when labourers are about. Although they destroy a considerable amount of produce, this farmer has never taken more serious steps against the animals than to attempt to poison them with apples injected with strychnine—a measure that has proved useless. Farmers in sheep districts declare that the most serious damage done by baboons is the destruction of "jackal-proof" fencing, while a forester informed me that the animals do incalculable harm in plantations by breaking off the growing tips of young trees. They are also said to spread the prickly pear bush, by conveying the seeds in their droppings. In the years 1925, 1926 and 1927, a bounty was offered for the scalps and tails of baboons in almost all parts of the country. In some districts this practice had been going on for a much longer period, and as many as two thousand rewards have been paid in a year in a single farming district. In spite of this slaughter, baboons are exceedingly common, and in most areas are not decreasing in number. They are still to be found on the outskirts of Cape

Town, which has now been settled by Europeans for some three hundred years.

These facts have an obvious bearing on the problems concerning the variations in the numbers of these animals. Theoretically, three factors are conducive to the increase of the baboon population of South Africa. The first is that in most places farmers are not hunting the animals extensively; the second, that their natural enemies, such as the leopard and other carnivorous mammals, have been almost completely exterminated in the farming districts of the country; and the third, that every new field that is planted becomes a potential feeding ground for them. In spite of these favourable circumstances there is no evidence to show that they are increasing in numbers. For example, a baboon pack which I observed twice in six years seemed to be the same size on both occasions, in spite of the fact that no more than about six of its members had been shot during the interval. Since every adult female baboon is able to reproduce at least once a year, and since man has not effectively assumed the rôle of a natural enemy, certain other factors must operate in keeping down the numbers of baboons. It is possible that one of these factors is famine. When vegetation and fruit are scarce, their ravages become even more impudent than they usually are; it is said that at such times they may steal eggs, and when this happens the farmer is perforce stirred into vengeful activity. Times of drought are also bad for the baboon. Impaled on the fence surrounding a dam on one of the farms I visited were a number of baboon skulls that had been recovered from animals drowned during a period of intense drought. The farmer's explanation was that baboons, frenzied with thirst, had come down to the dam in large numbers, and in the press and commotion some had been pushed in and kept under by their fellows. Disease usually assists in keeping down the numbers of most animal species, but whether or not any epidemics occur among baboons is unknown. None has ever been

reported to my knowledge, and none of twenty-five wild baboons I obtained during my visit showed any pathological lesion. All, however, were infected with tapeworms and round worms. Since none of the above-mentioned factors seems to be important in limiting the numbers of baboons, other explanations of their failure to increase have to be sought. It is possible that the fertility of baboons is low—a possibility that is not supported by observations that have already been recorded *. It is more likely that a considerable number die young, a view that is supported by observations of captive animals, and that a large number of adults are destroyed in baboon fights; without exception, every adult animal I obtained showed signs of such fights. The extent to which fighting occurs is unknown.

So far as I could discover during the time at my disposal, each pack of baboons keeps to the same area, which may not be very extensive. On one farm that was visited, a pack of about twenty-five animals was separated from another by a valley about three miles wide. I did not discover whether the two packs ever united. As is described below, the party that I studied had a fairly regular daily cycle of activities and seemed to travel over the same route continuously. Six years before this visit, I took part in a hunt presumably directed against the same pack on the same series of hills in which it lives to-day. Moreover, I was told by the owner of the farm that the animals have lived there for at least the forty years he has known the district. Similar information is given by most farm owners. One, however, told me that when he first settled a farm on a hilly, arid plateau covered with mimosa, cactus, and euphorbia, baboons commonly approached his homestead. After continuous and persistent hunting, their numbers have dwindled and they are seldom seen now, although they still can be found in small parties. This farmer was by far the most active hunter of baboons I met, and in one year was instrumental in killing two hundred and seventy.

* See p. 49.

The only record of migration known to me is mentioned by Fitzsimons, who reports that during the late winter of 1914 about five hundred baboons left one chain of mountains, near the small town of Ceres in the Western Province, to take up their abode in another.

On one farm where observations were made, a pack of baboons slept in different rocky outcrops on successive nights, apparently settling wherever they found themselves towards evening. Advantage is taken of this habit in preparing for a hunt. Beaters surround a pack and by shouting and shooting drive the animals so that at nightfall they find themselves near some particular rocks in which they settle. This outcrop has been previously girdled with heaps of dried wood. The animals are surrounded next morning before dawn while they are still in the crevices in which they settled the previous evening, and the wood is fired. The flames light up the rocks and apparently frighten the animals, which normally would not stir until daybreak. As soon as they move they are fired upon. Though some may escape from the ambush, this method of hunting is generally successful provided that the animals have been effectively driven the evening before.

A large pack of about one hundred animals may occupy more than one rocky cliff or krantz when it settles for the night. During the day the baboons may at times have been widely scattered, but towards evening they reunite and huddle in small parties in crevices that nearly always open on to a slope. Many of the sleeping parties which I observed appeared to include more females than males. Baboons apparently do not travel far when molested towards evening or during the night. One large pack that was disturbed soon after it had settled was occupying the crevices of a broken-up krantz about a quarter of a mile wide. Silently the animals tumbled out of their sleeping-places, and all made off in the same direction. There was no obvious leadership; the animals moved in a body to a near-by ravine, and it was not until they had resettled that they

were heard barking. The barks of the Chacma are almost indistinguishable from those of the Hamadryas baboon,* and I recognized the grunts of satisfaction made as the animals huddled together, and the threatening call of a single adult male, supported occasionally by the angry voices of some females.

Two evenings before, a pack of from fifty to sixty animals had been accidentally located as they came to rest for the night, and a party was collected to surround them in the dark. The krantz in which the baboons had settled was strewn with many loose boulders, one of which was set rolling, with a loud clatter, just as the sleeping animals were approached. A baboon barked once; a few seconds later there was the squeal of a baby, and then there was complete silence. Within five minutes we were in their recently vacated sleeping quarters, where we spent the night. Before dawn next morning, we moved off in the direction in which we supposed the baboons had gone, and again disturbed them where, to my surprise, they had settled some two hundred yards to our left.

For nine days I observed the movements of a pack of baboons that consisted of some twenty-five individuals, about half of which were immature. There were three fully adult males in the troop. The biggest was accompanied by four females, one of whom showed full swelling of her sexual skin during the period of observation; two females carried young. During the nine days they were observed the animals always spent the night in the neighbourhood of a particular prominent rocky face. They used to leave this krantz soon after dawn and make their way to the base of the valley, whence they moved over a distance of about three miles to a small ravine rich in prickly pear. Here they stayed for a considerable time, and then slowly proceeded to the crest of some hills above the ravine, where they spent hours moving about and rooting. Sometimes they revisited the prickly pear ravine later in the day, returning to their

* See Chapter XVI.

sleeping-quarters before sunset. Their movements were so regular, particularly in the early part of the day, that I could always be certain of finding them in the gorge of prickly pears at about eight in the morning, and by taking up a position somewhat earlier, they could be observed approaching across the foothills. Usually they came over the crest of the ravine in a body, but on one occasion the main party was preceded by a young adult male, who rushed in clattering on the stones like a galloping horse. Sounds of squabbling could often be heard before the baboons were seen.

My periods of observation in the gorge of prickly pears were usually curtailed by unsuccessful attempts to shoot females for anatomical purposes. Before they were disturbed the baboons seldom played in the shadow, but moved slowly with the sun as it crept to the side where the prickly pear mostly grew. The adult males were more sedate than the females, while the young animals were the liveliest, pursuing each other squealing over rocks and through bushes. Every now and then the noise increased, and sometimes I recognized the sound of an animal being chastised.

Sexual activities were much in evidence. Females presented to their males as they passed them, and were covered for a moment. Young males presented to each other, to females and to the older males. A female carrying a baby on her back walked slowly a little distance behind a big male, followed by a young immature male who occasionally caught up with her to tug her tail and touch her loins, as though he were about to mount. Now and then some animals settled for a while on the rocks in the sun, and picked over each other's fur, grunting contentedly. Sometimes the big males would move a short distance from the rest of the party.

Apart from the obvious dominance of a few of the animals, there were no clear signs of leadership in the movements of the troop. When disturbed the animals began a succession of barks, the voice of one appearing to

stimulate another, and they always escaped from the ravine in the same direction. Once the leading baboon was the female with full swelling, closely followed by an adult male. On another occasion this male moved off with his four females in a close party. Every animal, with hardly a moment's hesitation, fled in the same direction as his fellows. There were none of the directing cries one so commonly hears in the anecdotal literature. On two occasions, when the animals were disturbed by noise and not by shots, they did not move off very rapidly, and once two immature animals that seemed to be males hung behind on the crest over which the rest of their party had fled, swinging on a fence that passed over the mountain at that spot. They barked every now and then, and sometimes peered in the direction that their fellows had taken. After about ten minutes, an almost fully grown male returned and barked for a long time, finally disappearing with the two younger animals.

When they were disturbed the baboons always fled towards the crests of some hills that lay about two miles behind and above the summit of the ravine of prickly pears. Usually they moved very quickly, some animals covering this distance in less than ten minutes. The party did not hold together during its flight, but scattered over an area of quite two square miles. The separated animals barked every now and then, in that way, no doubt, acquainting their fellows with their positions.

Through powerful glasses, I watched their movements on the far hills for many hours on successive days. The animals spent a great deal of time grooming each other's fur. Usually the members of picking pairs changed about fairly quickly, but often I saw one pair sitting together for a full hour. Every now and then animals would be observed mounting each other, and on one occasion an adult male presented to another, who immediately covered him.

Most of the baboons moved about and sat on the crest

of the hills, but often some would rush down the slope making a noise and clatter that was audible to me a mile away. An animal would suddenly pursue one or more of its fellows, chasing in circles round some bushes. Once I saw the female with full swelling being pursued by the big male with whom I had previously observed her, and at other times the bigger baboons were seen chasing their immature fellows. In the midst of the chase they would suddenly stop, and often the three or four animals who had been in one chasing party, would separate after the excitement had died down. I could see no obvious reason for these activities, and came to the conclusion that they probably represented "play". But it is possible that they were squabbles arising out of the search for food. Similar meaningless running activity is often observed amongst the baboons on Monkey Hill in the London Zoological Gardens.

When not engaged in social activities the baboons dug, apparently for edible roots, foraged in low bushes and turned over stones, behaviour that is probably the basis of their reputation as scorpion hunters. Small holes that the baboons had dug were seen on almost every path in the Pirie forest, where I also searched for the animals. The holes had a characteristic shape, one side being vertical, the other sloping, in the direction that the animals had scooped with their hands. Since many of the holes were arranged along an obvious line and since one could see the direction in which they had been dug, it was possible to tell the way the herd had gone. When foraging, the members of a herd may separate over a wide area, but I did not obtain any indication that they ever post sentinels.

The observations made on this pack of twenty-five animals were supplemented by my experiences in other parts of the country. Fairly clear evidence was obtained that the larger troops are composed of several family parties. Mention has already been made of a troop of animals which when disturbed at night moved on only some 200 yards. About dawn the pack was

again disturbed and broken up into isolated animals and small family parties, one of which, consisting of a large male and four females, passed within ten feet of me. The separated animals remained apart, sometimes barking, for several hours, and finally came together on the opposite side of the valley. Another big pack that was hunted one morning in the same district also divided into numerous smaller parties. Individual harems could be recognized; adult males could be seen wandering alone, while immature animals were widely scattered, some of them keeping together in small groups.

In another region of the country, I took part in two hunts that were organized in the manner described on page 199. During a preliminary drive, a party of eight baboons consisting of a single adult male, adult females and young, was encountered, but on the occasion of the hunt it was believed that a considerable pack had settled down for the night within the ring of prepared fires. As soon as the fires were lit and the guns were in position, the native beaters who were tending the flames began a fearful din, in response to which only a single baboon barked. About three of the ambushed animals tried to escape when it became light, but they were met by a volley of shots which brought down one, an adult female. Shortly afterwards an adult male, followed by two females, tried to escape. The females were killed, but the male succeeded in escaping. No other adult male was seen, and only a few females and immature males succeeded in escaping subsequently. The morning's bag consisted of twelve adult and two immature females, and one immature male. Three of the twelve adults were nursing, and in each case the baby was pulled, protesting, from its mother's fur, to which it was still clinging after her death. The young animals were quietened by replacing them on the carcases, to none of which were they specifically attracted. Each baby seemed quite as happy clinging to the immature male as it was on any of the adult females. A week later a hunt on the same spot proved relatively un-

successful. Only one adult female and an immature male were shot, but again a big adult male was seen escaping. It seems fairly certain that on the first hunt only a single harem, containing one adult male and at least twelve and possibly as many as twenty adult females, had been ambushed. The animals killed on the second hunt were possibly the survivors of the first, or perhaps a few stragglers from another pack unsuccessfully ambushed. It is a fair assumption that male and female baboons are born in nearly equal numbers,* and, unless there is a considerable post-natal mortality amongst males, the presence of more than twelve females in a single harem indicates that a number of males in this district live either in solitude, in male bands, or possibly in a larger herd containing other harems. Such a herd exists in the neighbourhood, and it seems possible that the harem that was hunted had separated from it.

An extraordinary account of baboon life, entitled "Baboons, Hypnosis and Insanity," was published in *Psyche* [246] in 1926. The author, E. N. Marais, states that he lived in Waterberg among a wild troop for over three years, taming them sufficiently to render close contact possible and safe, and naming and numbering each adult of the troop. No hint is given of the method by which the animals were tamed. The size of the troop is not stated, but according to the author it was "dominated by a council of ten old males and one barren homosexual female (with secondary male characteristics)." Again the author does not indicate the nature of the secondary male characteristics that this female displayed—a regrettable omission, since this observation is unique in the field of sub-human primate anatomy. In the midst of many somewhat obscure statements that appear in the article, Marais mentions one which, if authentic, is of some interest. He writes, "masturbation was a common practice among the young males deprived of females, even under natural

* See Chapter XIII.

conditions." I myself did not observe this behaviour amongst the baboons I encountered.

Many accounts have been published in which reference is made to sentinels placed by baboons during their foraging and pillaging activities. The use of the term "sentinel" is altogether unjustifiable. There is no evidence of any kind that special members of a troop are placed on its outskirts for the specific purpose of "doing sentry-go", and so far as can be observed, any baboon of a pack who happens to see an approaching human being will bark. Moreover, all careful and experienced observers agree that a man may often stumble close upon a pack of baboons when passing over a ridge on one of their rocky hills. Such accidental encounters could hardly be possible if sentries were posted in the manner suggested in some accounts.

Baboons are also reputed to be extremely ferocious, but this again is a belief that will not bear close examination. My experience is that when attacked they respond by flight. On many occasions I have come up very close to them, and they have never shown fight. It may well be, however, that baboons do sometimes attack men after provocation, in the same way that any animal will turn upon its tormentors. Stevenson-Hamilton,[337] for many years the game warden of the National Park in South Africa, writes that "in general practice, baboons no less than other wild things habitually give way before man, and not being flesh-eaters, they have seldom any natural inducement to make attacks upon other mammals." There can be no doubt that both domesticated and wild animals move without any display of fear in the neighbourhood of baboons. A lamb was reported to have lived for some time in a troop of baboons,* and I have seen Chacma baboons playing about and foraging in the midst of a flock of Persian sheep grazing high upon a mountain side—observations that lend little support to the belief common in South Africa that baboons tear

* See *Cape Argus*, April 26th, 1930.

Photograph by F. W. Bond

A YOUNG BABOON WITH FILLED CHEEK-POUCHES
(See p. 234)

[*face p.* 206

open young lambs. Loveridge,[239A] as I have already noted, has recorded instances in which baboons foraged in the company of wild pigs and bushbuck. It seems likely that, apart from their response to the attacks of their natural enemies, whatever ferocity baboons display in their own surroundings is expended mainly among themselves. Such reports of child murder as have been mentioned on page 195 require corroboration before they can be accepted. Reports also exist of human children being abducted and reared by baboons *—stories very reminiscent of the "wolf children" of India. These tales seem closely related to the tradition that gorillas, baboons—in fact, all the bigger primates—rape native women. Other accounts tell how baboons hurl stones when attacking, but whether or not these reports can be accepted is doubtful. Throwing loose objects is certainly not a frequent activity of captive primates, and when exhibited, does not seem to be an effective form of attack. It is quite likely that the movements of baboons on rocky hills dislodge loose boulders which may thus be set rolling and hit human onlookers. So far as I am aware there is no authentic report of wild baboons actually picking up stones in their hands and throwing them.

* See *Johannesburg Sunday Times*, October, 1930.

CHAPTER XIII

THE SOCIAL GROUPS OF WILD APES AND MONKEYS

SO far as can be judged from the accounts of monkeys and apes discussed in the two preceding chapters, the harem forms an essential element in the social lives of wild sub-human primates. The accounts that have been considered are mainly of three kinds. There are those which definitely point to the occurrence of polygyny or of monogamy. From these it is clear that the greater number of apes and monkeys about whom there are definite data are polygynous (the few exceptions being the smaller South American monkeys which are stated to live in pairs).* Other reports do not give any direct indication of mating habits, but simply relate that although a species is found usually in small or big parties, lone males are also encountered. The latter fact is the only available clue to the constitution of the parties, for since, as a rule, the sexes are born in equal proportions, one can infer that the groups contain more females than males—an inference suggesting polygyny, and one that is supported by the fact that polygyny maintained by dominance is the habit of captive monkeys. The third kind of report that has been consulted only indicates that certain species are gregarious.

The balance of the evidence quoted suggests that most, if not all, wild primates are polygynous or tend to

* Attention may again be drawn to Allen's observation [17] of a solitary female capuchin (see p. 191). This is the only observation indicating that a female monkey was separated from a male that, to my knowledge, has appeared in the literature.

polygyny. In the search for an explanation of this habit, two factors must be considered, namely the sex-ratio and masculine dominance. The extent to which polygyny occurs in such species as baboons, gorillas, and howler monkeys suggests the possibility that fewer males are born than females. Wislocki [380] has published a table showing the proportions of the sexes in monkeys of all ages shot in the forests of South America.* The sex-ratio of eighty-nine spider monkeys is fifty-one males to one hundred females; of one hundred and seventy-nine howler monkeys, seventy-seven males to one hundred females; of fifty-two capuchins, one hundred and eight males to one hundred females; and of forty-six titi monkeys (genus *Saimiri*), one hundred and nine males to one hundred females. Wislocki suggests as a possible explanation of the uneven ratio in the spider and howler monkeys that "fewer males than females are produced in these species due to an uneven sex-ratio in the germinal cells." This is a highly speculative suggestion, since Parkes,[279] who has reviewed the problem of the proportions of the sexes in mammals, came to the conclusion "that the general nature of the mammalian sex-ratio is essentially one of equality." Wislocki has also suggested that the disparity between the numbers of the sexes of his monkeys may be due to a higher post-natal mortality amongst the males than amongst the females. This is a more likely explanation, but a still more important factor has first to be considered. Contrary to Wislocki's opinion, it is possible that even though they "were shot without reference to selection", his specimens cannot "be relied upon as giving a true picture of the natural population." Although no field notes relating to the shooting of the animals are provided, it is safe to speculate that fewer solitary animals were shot than were animals in parties—for the obvious reason that a party

* The ratios quoted here are calculated from Wislocki's tables, and the figures given for two of the four species are different from the percentages he gives in the text.

is more conspicuous than a single animal. His data thus probably refer not to the entire population of howler and spider monkeys, since in all likelihood they ignore those animals that live in solitude. This possibility is borne out by Wislocki's own figures. The eighty-nine spider monkeys he discusses consist of sixty-five adults, the rest representing a variety of immature stages. Ten of the twenty-four immature specimens are males, whereas only twenty of the sixty-five adults are of that sex. Similar inequality in the sex-ratio is shown when the immature and mature specimens of howler monkeys are considered. Twenty of the thirty-eight immature animals are males, whereas of the one hundred and forty-one adults only fifty-eight are males. Wislocki's figures do not therefore give a true picture of the natural population, unless one imagines that an enormous number of males as they reach maturity either perish from exposure and starvation, are destroyed by carnivorous animals, or are killed by their fellows. It is possible that a certain number are eliminated by these means. As was suggested in the last chapter, it seems very likely, for example, that many baboons die before reaching maturity, and it may well be that the number includes a larger proportion of males than females. The females, as is indicated in a later chapter, are probably included in harems from a very early age and move under the immediate protection of adults. On the other hand, young males lead a much more independent life, and it is possible that they are more readily lost, to perish. It is also conceivable that males are more adventurous than females, thus becoming more exposed to the attacks of carnivorous animals, and that adult male monkeys kill each other in large numbers in sexual and other fights.* But a much more likely explanation of the large number of female monkeys that are shot, as has already been suggested, is that female monkeys are encountered in

* In captivity, see Chapter XIV, a far greater number of females are killed than males.

parties in which their numbers preponderate and that a large number of adult males lead a solitary life and usually escape the notice of hunters. The evidence for a real preponderance of females amongst monkeys and apes is by no means established. In the present state of knowledge an unequal sex-ratio cannot be accepted as the determining factor underlying the tendency towards polygyny.

That masculine variability within the species is an important factor determining the distribution of females is shown by the following data about captive baboons. In the colony of Hamadryas baboons living in the London Zoological Gardens at the beginning of 1929, eight of thirty-nine adult males possessed the only nine females, one male having two. It might have been said that monogamy was the prevailing rule in this group of animals. On the other hand, in a similar baboon colony that consisted of twenty-five adults of each sex and about one hundred sub-adults, living in Munich in December of 1928, five males possessed all the females, one owning seven. This colony was reduced in size, and in April of 1929 consisted of eight adult males, ten females, one of which was immature, and forty-two male sub-adults. Four of the adult males owned all of the females, one having four, another three, a third two, and the fourth one. Such irregularity in the distribution of females can depend only on variability in those qualities which go to make masculine dominance. It is difficult to say what they are. Size is certainly not the only factor involved, for a larger male baboon is often dominated by a smaller. Better canines and agility in fighting might possibly be important factors. Masculine dominance is not, however, a problem for speculation, since clearly it could be examined experimentally. In whatever way it is brought about, dominance is clearly a factor of the greatest importance in determining the extent of polygyny within a species.

Monogamy and polygyny may exist side by side in

the same species, since they depend on the distribution of those qualities that go to make masculine dominance. Equality among the males of a group inhabiting a particular area might result in the formation of a number of "monogamous" families. All primate species exhibit great individual variation in these qualities, and it is possible that those species in which monogamy is more frequently observed are those that exhibit a lesser degree of masculine variability.

It seems possible that sexual dimorphism is a factor that should also be taken into account when considering the distribution of females within a social group. Observations that are recorded in the following chapters indicate that the female lower primate is completely dominated by her male overlord, and her subjugation may well depend upon his physical superiority.* The males of all primate species are larger than the females, by amounts that vary from species to species. Thus, there is a much greater difference in size between the females and males in the species of baboon and in the gorilla, than there is in the species of gibbon and in the chimpanzee. It may be significant that there is a widespread belief that the gibbon and chimpanzee are more monogamous than the gorilla and baboon. It is possible that sexual dimorphism plays some part in determining the monogamy or polygyny of a species, but in the absence of evidence such a view is purely speculative.

Because of the difficulties of observation it is doubtful whether knowledge of the average length of time that a family party of primates holds together in the wild will ever be available. My own observations of captive baboons indicate clearly that a family endures only as long as the male overlord maintains his dominant position, the period varying, therefore, with different individuals.

Some species of primates appear to live in isolated families; others, like the baboon, usually live in enormous

* As it does in the lower mammal. See, for example, Stone.[338]

hordes consisting of numerous families banded together. The distinction between the two modes of life is, however, by no means rigid. Single baboon families are frequently encountered, and there is no evidence to show that they do not constantly split off from a larger troop in the way that the gorilla family is reputed to do. It is perhaps noteworthy that, with the exception of the hoolock and siamang gibbons, species of primates living in the heart of the forest away from human beings, are those that are reported to live in single families. Those living away from the forest zone, coming into close contact with man and pillaging his farms, are those which live in bands of several families. There is no available information to show whether the larger primate band is, however, a firm social unit. Though it reacts offensively to the introduction of new members, it is not so "closed" a group as is the family.

As is described in the following chapters, no adult male except the overlord enters into sexual relationships with the females of a family group. Those male monkeys and apes who are either permanently or temporarily without females spend their celibacy in a variety of ways. Some of them are the "lone males" that are occasionally encountered. Others, like the Entellus langurs, appear to live gregariously in male bands. Still others, like baboons, may be included in the large troops formed by the union of numerous family parties. Their presence in these herds is possibly due to the fact that female primates act as a centripetal force attracting males. As was stated in an earlier chapter, adult male sub-human primates are always sexually potent, and adult females are always to some extent sexually attractive. Permanent sexual associations can obviously be considered to be an overt expression of these powerful physiological conditions. The harems themselves may be regarded as an effect of life in this type of association. Males probably learn by experience that unless they hold their females by exercising their dominance their own sexual

responses might be effectively inhibited by other males. This constant attraction of the females for the males may also be one explanation of the occurrence of large hordes of monkeys, the females of harems attracting to their vicinity both unattached males and the males of other family parties, even though there is no overt expression of heterosexual interest except within the family.

It is unfortunate that neither the available naturalistic accounts that have been quoted, nor my own observations of wild baboons, provide data for more detailed consideration of the social behaviour of subhuman primates. For the further discussion of this question, to which the following chapters are devoted, reference has to be made to observations of the social behaviour of captive apes and monkeys. The conclusions that have been drawn here about the behaviour of wild primates form a framework into which observations of captive animals can be fitted.

CHAPTER XIV

THE HAMADRYAS BABOON COLONY

THE only descriptions of sub-human primate socio-sexual behaviour hitherto published have concerned small groups of animals, whose relationships were experimentally arranged by their observers. Three of these accounts are of especial interest. Hamilton,[136] who was the first to report observations in this field, studied a group of twenty animals consisting of different kinds of macaque (*M. rhesus* = *mulatta*, *M. irus* = *cynomolgus*, *M. sp.*) and two baboons (*Papio sp.*). The results of his investigations were published in 1914. Köhler's[217] studies on anthropoids, carried out between 1913 and 1917 in Teneriffe, are more widely known. Though chiefly concerned with problems relating to intelligence, he also made interesting observations on the social life of a small group of chimpanzees, most of which were immature. A more important investigation of the same problems was carried out by Bingham.[40] His account, published in 1928, deals with the early sexual adjustments of four immature apes.

The investigations carried out by these observers have yielded a rich harvest of facts concerning sub-human primate socio-sexual responses, even though these studies have perhaps been limited by their experimental nature and the scarcity of their material. A full display of the naturally orientated sexual responses of any sub-human primate species could only be observed in a homogeneous and complete group of animals—a group consisting of individuals of all ages and both sexes, preferably from the same locality. The true significance of many forms of sexual behaviour,

which appear meaningless when manifested in a cage, can be readily recognized in a social environment of this kind. Opportunities for studying such social groups have only recently arisen.

Colonies of Hamadryas baboons (*Papio hamadryas*), living under conditions that reproduce their natural environment as closely as possible, have in the past few years been exhibited in many zoological gardens. The plan followed in most institutions has been to free from fifty to a hundred baboons of both sexes and of all ages in a large enclosure, the surface area of which is increased by artificial hills and rocks. By means of a system of trap-doors it is possible to shut the animals in their sleeping quarters, which are usually either within the rocks or in adjacent cages. Arrangements are also made so that one or more members of the colony may, if necessary, be isolated from the rest. The enclosure is cleaned daily, and apart from the maintenance of a regular food supply, the baboons are not subjected to active interference. They are allowed to determine their own social and sexual relationships.

The common belief that the new environment grossly distorts the expression of these relationships has no foundation in fact. The pattern of socio-sexual adjustments in captive colonies is identical with that observed among wild animals. Moreover, the elements of social behaviour exhibited in one colony differ in no observable manner from those of any other. This could hardly be expected if socio-sexual activities in confinement were merely a reaction to unnatural conditions. If they were, one might reasonably suppose that the environmental dissimilarities of different colonies would stimulate slightly different forms of social behaviour. It might also be expected that an experimental stage in which behaviour took many forms would precede a stabilization of social responses. This does not occur. Behaviour is uniform in all phases of the history of these colonies. Con-

siderations such as these indicate that socio-sexual adjustments are determined by the mutual responses of the animals, and not by environmental influences.

Feeding is a field of behaviour in which the effects of artificial conditioning are obvious. Baboons will at all times eat almost any food except meat, and in confinement they are always on the watch for the offerings of onlookers. "Conditioned reflexes" may be established through feeding by habitual visitors, whose particular baboon "friends" will immediately make for the part of the barrier they approach. Such a "reflex" is always established between the members of the colony and their keepers. It is conceivable that an assured and constant supply of food has important effects upon the behaviour of captive animals, since it provides leisure that would otherwise have been expended in foraging over a large tract of country. An excess of energy may therefore be liberated for expression in other channels, and sexual behaviour may perhaps be intensified. Even if it is, there is no reason for supposing that it is artificially perverted.

It is also possible that captive conditions modify fighting behaviour. Confined to a small area animals cannot separate from one another as they would in a natural environment. A baboon worsted in a fight is unable to escape from his aggressors. An animal not dominant enough to maintain himself and his harem in a large herd cannot succeed in retaining his females by avoiding contact with his fellows, as he might in a wild state. These considerations suggest that fights may often be carried much farther in captivity than they would be in nature. This, however, adds to their interest. From the point of view of the observer, confinement concentrates a normal response both temporally and spatially.*

The difficulties attending observation of the movements of individual baboons in a large herd are not so

* See p. 220 concerning the effects of an uneven sex-ratio on social stability.

great as might be expected, since the animals differ considerably in appearance. Recognition of individual members is simplified by variations in coat colour, by differences in hair growth—often the result of injury—and by the presence of scars. Face colour sometimes varies, and animals may show special peculiarities such as warts. These individual characteristics are usually superimposed upon more subtle, but significant, differences in bodily form.

In the spring of 1925 the officials of the Zoological Society of London liberated about one hundred Hamadryas baboons (*Papio hamadryas*) in a large oval rock-work enclosure one hundred feet long and sixty feet wide. There are two main piles of rock on "Monkey Hill", each enclosing cave shelters, which are fitted with electric heating arrangements. The entire structure is surrounded by a wide ditch. So far as can be seen from existing records, all but six of the original animals were males, most of which were adult. The first plan had been to maintain a purely masculine colony, but the accidental inclusion of the six females, which subsequently bred, encouraged the Society's authorities to import others. On the 27th of June, 1927, two years after the Hill was founded, the existing population was accordingly augmented by thirty adult females and five immature males. Two other animals, a female and a male, had been added before this batch was purchased.

Sixty-two males and thirty-two females died during the six and a half years following the foundation of the colony, and autopsies were performed on almost all the bodies. Between June and December of 1925, there were twenty-seven deaths, twenty-six from recognizable pathological lesions of internal organs, and one from injuries received in fighting. Many of the animals whose deaths were attributed to organic disease also showed wounds indicating their recent participation in fights. For example, one animal, both of whose lungs were in a pneumonic condition, had a suppurating

PLATE XVI

Photograph by J. F. Saunders

A MALE BABOON EATS MACARONI, HIS FEMALE MAKING NO ATTEMPT TO SECURE ANY

(See p. 235)

wound on the left forearm, which may have been inflicted before or—since sick baboons are often attacked by their fellows—after the onset of its fatal illness. In 1926, two males and a female were killed by their fellows, and four males died. Early in 1927 the stock was still further depleted by the deaths of six males, and of one female who was killed by her companions. The remaining population was only fifty-six when the new batch of females was introduced in June of that year. The new arrivals stirred the Hill into great excitement, and all the old males tried to secure females, fifteen of whom were killed in the fights that occurred between the 27th of July and the end of August. These fights are definitely sexual in nature. The males fight for the females, who are usually fatally injured in the mêlée which rages around them. By the end of December the population was even more reduced by deaths from disease and from injury, and at the beginning of 1928 it consisted of fifty-one males and fifteen females. By the end of the year (1928) the colony had again been thinned by the deaths of nine males and four females. In January of 1930, the troop numbered thirty-nine males and nine females, one of which is the only survivor of all the animals bred on the Hill. During the year three males died and four females were killed. The fight in which the last of these females lost her life was so protracted and repellent—from the anthropocentric point of view—that the decision was made to remove the five surviving females from the Hill. These were separated from their "overlords" with some difficulty, and since October, 1930, the Hill has been populated only by males, of whom there are now * thirty-four, only one of which is immature.

Eight males in all died from injuries received in fights, and fifty-three from disease. Most of the more common pathological lesions have been found at post-mortem examinations, such as valvular disease of the

heart, atheroma, pericarditis, pneumonia, pulmonary abscess, pleurisy and empyæma, enteritis, colitis—often ulcerative—pancreatitis, peritonitis and nephritis. A few animals were infected with worms, one died of generalized mycotic infection, and others from septicæmia. Tubercular lesions have never been found in animals that have died on the Hill.

Of the thirty-three females that died, thirty lost their lives in fights, in which they were the prizes fought for by the males.* The injuries inflicted were of all degrees of severity. Limb-bones, ribs, and even the skull, have been fractured. Wounds have sometimes penetrated the chest or abdomen, and many animals showed extensive lacerations in the ano-genital region. At least four of the females killed were immature. A few that met their deaths within a few days of their arrival were at the time suffering from organic disease, and two died shortly after miscarriages apparently precipitated by fighting. The injuries sometimes appeared to be too insignificant to have caused death, which was then probably due to exhaustion, since "sexual fights" may be prolonged for several days. No lesion was found in one of the three females that died "natural deaths". The other two died of pneumonia, complicated in one case by parturition.

The greatest number of deaths occurred in 1925

* See Chapter XVI. It is difficult to believe that so large a proportion of females would be killed in a natural community, even though there can be no doubt that wild female baboons are also exposed to the attacks of their fellows. Thus scars were seen on practically every carcase of an adult female baboon that I obtained in South Africa. The very high percentage of females killed in the London Colony suggests, however, that the social group of which they formed a part was in some way unnatural. It seems reasonable to suppose that family parties were thrown into contact with unmated males far more than they would have been in the wild. The unmated males were continuously and probably unnaturally exposed to a situation conducive to social disruption. It is possible, therefore, that the London Colony would have been more tranquil had there been five times as many females as there actually were—or if there had been greater disparity in the size of the males.

and 1927, when the main consignments of animals were introduced. Twenty-six animals belonging to the 1925 batch died of disease within three and a half months of their arrival, and fifteen of the thirty females imported in 1927 were killed within a month. Judging from the total records of females that died from injuries, fighting seems to have occurred throughout the year. Because of their small number it is impossible to decide whether or not any significance attaches to the fact that the only eight males that were killed lost their lives in the autumn and winter. On only two separate occasions have males and females been killed in the same fight. Two males, an adult female and an immature female born on the Hill, died from injuries inflicted by their companions between the 22nd of February and the 2nd of March of 1928, and a year later an adult male and an adult female were killed in another fight. Deaths from disease, excluding those that resulted from infections probably contracted before the animals arrived in the Gardens, have occurred oftener in December than in any other month.

The abnormal number of deaths that followed the introduction of the two main groups of animals have clearly to be disregarded in the consideration of the possible effects that the death of any one animal has upon the stability of the colony as a whole. When this is done, the records suggest, as the following examples show, that a frequent result of such an event is social discord. Early in 1927 a young female was killed the day after three males had died. In February of 1928, a male, whose body showed the scars of recent fights, died of pneumonia: four days after its death a male was killed, and two days later a second animal died from injuries. On two separate occasions in 1929 a female was killed in less than a week after the death of a male, and in 1930 one female was killed within four days of the death of another. The number of fatal fights that have followed deaths on the Hill is too great to be without significance, and the meaning

of the correlation is obvious. The equilibrium of a social group is dependent upon the mutual reactions of all its members. The death of any single individual upsets the state of balance, and fighting commonly breaks out before a new equilibrium is reached. It must be emphasized that fights in which deaths occur are rarer than those that do not lead to a fatal issue, and of these there are no records. Hence, it seems safe to infer that the amount of fighting that occurs in phases of social rearrangement is greater than is indicated by the number of post-mortem examinations.

At least fifteen baboons have been born on Monkey Hill, and all but one of these have died. In most cases—if not all—death occurred within six months of birth. With few exceptions their bodies were not recovered * and only five autopsies have been performed on these young animals. These five all died of injuries. Observations made on the Hill show that the young animals often die of strangulation. A young baboon clings to the hair on the belly of its mother, who supports it with her arms. When a quarrel breaks out on the Hill, excitement may spread to all the animals, most of whom will then make for the centre of the fight. In the mêlée it is possible that a nursing baboon tightens her hold on her clinging infant and thus strangles it. There is a record of a nursing animal that dropped her baby in the excitement of a fight. The young animal was immediately seized around the neck by a male, who made off with it. It died as a result of this series of adventures. Another death, which I observed, was caused deliberately by an adult male who, during an attack on a female, suddenly transferred his attentions to the baby she was carrying, injuring it severely in the loins.† Sometimes there is no apparent reason why a baby has been strangled; it may be simply due to the inexperience of the mother. For example, one female appeared to be extremely careless with her baby. Instead of holding it

* See Chapter XVIII. † See p. 245.

gently, she either clasped it roughly and pressed it tightly to her body, or placed it beside her on the rocks—a very unusual method of treating a newly-born monkey. Just before it died, the young animal could be seen gasping for breath as its mother squeezed its chest. The only baboon bred on the Hill that is still alive is a young female that was born in October of 1928. Her history is discussed at a later stage.

The growth phases in the life of the baboon are not well known. About a fortnight after birth a young animal leaves its mother and tries to walk. Solid food becomes a recognized part of its diet when it is a month old. The young baboon's movements gradually become well co-ordinated, so that at about six months its range of muscular activities is very extensive. Puberty is reached when the animal is probably between four and six years old. The total length of its life is unknown. Flower has a note about a male Chacma baboon that lived forty-five years in captivity. He also mentions two Hamadryas baboons that "appeared very flourishing after twenty-four years in captivity", though he gives as his opinion that the males of this species attain their full size and strength when eight to nine years old, and that they continue in their prime to thirteen or fourteen years old, after which they may begin to show signs of senility. The "prime" of a baboon, one may add, depends not only upon its muscular vigour, but also upon the wear of its teeth.

My own detailed observations of the London colony of baboons on Monkey Hill began early in 1929. Observations were also made on two separate occasions, totalling seven days together, on a Hamadryas baboon colony in the Tierpark in Munich. Since my observations of behaviour in the Munich Colony, the constitution of which has been noted on page 211, agreed in detail, so far as they went, with those made in London, the following descriptions cover the behaviour of both

colonies.* Before these descriptions are given, mention may be made of some outstanding events that occurred on Monkey Hill in 1927 and at the end of 1928.

Attached to the account of the autopsy of a female that died in January of 1927 is the note that "four males fought over her, and the victor being set upon, dragged her into the water, where the fight continued. When it was finished, the female was found to be dead." This was the female referred to previously, who met her death the day after three males died. Judging by my later observations, it is safe to infer that she had been attached to one of these three males. His death released her as a prize to be fought for by the remaining males of the colony. Serious fighting broke out a little time before I began to keep a continuous record of the behaviour of the baboons on the Hill. On the 20th of December, 1928, an adult male

* A colony of Hamadryas baboons, originally consisting of 140 animals, was on view at the Colonial Exhibition in Paris (1931). There were 110 alive on the 23rd of September when I saw the colony. According to the Director of the Zoological Section of the Exhibition, thirty baboons had died, mostly in June and July, and death was attributed, in nearly every instance, to "la grippe". Only a few were said to have perished from wounds received in fights, which occurred almost daily but had been most frequent in the first weeks after the foundation of the colony. Of the female survivors in September, six, at most, were fully mature, the majority showing swelling of the sexual skin characteristic of puberty. Few of the males that had passed puberty, and had the adult coat, were fully grown. Judging from two hours' observation, the organization of the colony was as follows:—one male, the biggest in the group, owned eight females, three had three each, three had two each, and there were five monogamous family parties. The owners of the more mature females appeared to be the more powerful males. Some of the unattached sexually mature males were bigger than some of those that were mated, and a few of them accompanied family parties in their movements (see p. 226). A "bachelor" was not included in the largest family party. One mature and unmated male appeared to be attached to a younger male. The behaviour observed was identical with that described in the following pages. A "sexual fight" (see p. 253) was in progress, and the female of the monogamous family party around which it centred was severely lacerated. Several of the other females showed signs of recently inflicted injury.

died of pneumonia. Upon his death the female he had possessed was involved in a fight in which, nine days later, she lost her life. Another male died of injuries on the 2nd of January at a time when each of his two females was nursing a baby. These babies were strangled in the fights that raged around their mothers, one of which was killed, while the other was successfully seized by an unmated male. This account, which is based partly upon post-mortem records and partly on the testimony of keepers on the Hill, represents, to my knowledge, the only instance of a female changing hands since the stabilization of the colony following the introduction of the batch of females in 1927.

When regular observations were begun early in 1929, the population of the Hill was forty-one males, four of which were immature, and nine females, one of which was nursing the young animal that was born in October of 1928. These nine females were owned by eight males, there being seven "monogamous" family parties and one that was "bigamous". These relationships were stable. With little exception, there was no promiscuity. Five of the nine females lost their lives in fights caused by other males attempting their abduction. The last of these fights, which occurred in October of 1930, resulted in the death of one of the two females of the bigamous family party. Their overlord, a conspicuous member of the colony, had never, so I was informed by the keepers, owned less than two females. It was after this fight that the remaining four adult females and the immature female, together with an adult male, were removed from the Hill. They were isolated in a roomy cage, at first away from the view of the public. Opportunity was thus provided for more detailed observation of behaviour in a harem than was possible when the animals were on the Hill.

A family group consists of a male overlord, his female or females, together with their young, and may sometimes include one or more "bachelors" or unmated

males. The bachelors are not an essential element in the party, although they may be attached to it, according to my observations, for as long as a year. As is explained below, they appear to be held to the group mainly by their interest in the females, but it is possible that they are also attracted by the overlord. Bachelors have attached themselves more frequently to some of the harems on the Hill than to others, perhaps owing to the more complacent temperaments of some of the mated males. Family parties move independently of one another, and seldom come into contact. They act as separate groups in all their activities, as a rule mingling with other members of the colony only when engaged in communal feeding or when participating in some quarrel. Different groups maintain different degrees of isolation. Each party moves as a unit, and though the overlord usually takes the lead in these movements, any other member of the group may occasionally do so.

Throughout the year the females undergo cycles of sexual desire which are correlated with the rhythmical changes occurring in the sexual skin. Desire, as shown by changes in behaviour, is greatest when the swelling of the sexual skin is at its maximum, and it is at this time that the female is most attractive to the male. The "chief wife" in the harem is the female that shows greatest swelling, her prior position being manifested by the fact that she keeps closer to the overlord than do the other females of the harem. At such times she seldom moves away from him, although when her sexual skin is quiescent they may be separated by as much as twenty feet. The "chief wife" grooms him more than do his other females, and it is upon her that he concentrates his sexual activities. She is also allowed to take from a limited supply of food, although he would usually attack her if she were to do the same when her sexual skin is quiescent.

Copulation occurs as a rule only between an overlord and his females, on occasions being often repeated,

PLATE XVII

Photograph by F. W. Bond

MALE BABOONS FIGHTING—ONE AGAINST ALL

though sometimes incompletely, in a short space of time. It may be preceded by mutual manual and oral examination of the genitalia, though such examinations are often carried out independently of both grooming responses and direct sexual activity. Occasionally the male does not mount until after persistent presentation on the part of a female. Presenting must be regarded as a primarily sexual response. It varies in its expression from the full copulatory position to a slight turn of the body that might be almost imperceptible to inexperienced observers. In the full copulatory position the animal presenting stands with its hind legs fully extended, and with its body bent downwards from the hips, the head being away from the animal to whom the sexual presentation is being made. The less perceptible forms of presentation are usually seen when one baboon slightly moves its hindquarters in the direction of a fellow that it passes.

Baboons seldom mate during the quiescent phases of the sexual skin, that is to say, during the second half of the menstrual cycle, during pregnancy and during lactation, but a female is rarely observed to refuse the male. Frequently, especially in the phase of sexual-skin swelling, females persistently present and sometimes assume a crouched attitude, with the limbs bent and the ventral surface of the body pressed to the ground. This solicitation is frequently augmented by the female turning her eyes and fixedly regarding the face of her male. As he moves she may rub her body against his chest, and squeal in a high-pitched voice. The male may respond to this behaviour by mounting, but on the other hand, after repeated intercourse he frequently assaults his female with his teeth and hands, pulling at her hair and biting her, usually in the scruff of the neck. Different degrees of vigour can be recognized at different times in the sexual response of the male baboon, but it is difficult to decide whether these apparently sadistic attacks upon the female represent transferred

sexual responses or a fatigue reaction. On one occasion it was observed that a male instead of responding to the continued presentations of his female moved away a few feet and mounted a bachelor. Two minutes later he returned to his female, whom he then mounted. A female, after she had been persistently presenting and after she had been mounted five times within five minutes by her overlord, half mounted, in the masculine position, a bachelor attached to her harem.

Baboons are not promiscuous. Very few observations have been made of females having sexual relations with males other than their overlords. If serious attempts at abduction that led to fights are discounted, instances of infidelity have always seemed to occur when the overlord's back was turned. This behaviour has been observed on the part of only three females, two of which belonged to the bigamous harem, the third being a particularly assertive female who belonged to a very powerful baboon. None of these females has been seen to be "unfaithful" during a phase of sexual-skin swelling. This is easily understandable, since at such times the female always remains near her overlord, whom she follows closely. The quiescent phase of the sexual skin, when females may wander several feet from their overlords, often out of range of his vision, presents more opportunity for infidelity.

The situations in which the "monogamous" female proved unfaithful were very characteristic. On one occasion when her overlord's back was turned she quickly presented to the bachelor attached to her party, who mounted for a moment. The overlord then slightly turned his head, whereupon the female rushed to him, her body low to the ground, presenting and squealing, and threatening her seducer with grimaces and with quick thrusts of her hands on the rocks. This behaviour immediately stimulated an attack by the overlord who was apparently responding blindly to the "fear-threatening attitude" of his female. Closely pursued, the bachelor fled. On another occasion the

same female was left alone for forty seconds while her overlord chased a bachelor around Monkey Hill. In that space of time she was mounted and penetrated by two males to whom she had presented. Both of these immediately made off after their contact with the female, who again responded to the return of her male in the manner described above.

The females of the bigamous harem were party to most of the instances of infidelity that were observed on the Hill, the male involved always being a certain bachelor who was attached to their family group. In their case the "illicit" sexual response was manifested very hastily at opportune moments. For example, when the harem was on the move the overlord would lead, closely followed by his female in "heat", the bachelor and second female following a short distance behind. In such circumstances, with the overlord's back turned, the sexually quiescent female would sometimes be mounted. On one occasion, the pair was observed taking advantage of the confusion of a general mêlée, in which the overlord was interested, though not directly involved. Apparently the overlord never observed the "infidelity" of his females. On the rare occasions when both females coincided in the swelling of their sexual skins, both were assiduous in their attentions towards him and he divided his sexual and social activities more or less evenly between them. On many occasions females were observed in sexual relation with immature males in the full view of their overlords, who made no aggressive responses. The sexual activities of the mature females and the immature males varied from mutual genital examination to complete mounting and penetration. On one occasion, sexual activity of the latter kind was interrupted by the overlord moving off from the position in which he was sitting. The female immediately followed her overlord, carrying the young male with her.

Homosexual behaviour is frequently engaged in by

all members of the family group. Mutual grooming, genital examination and mounting may take place between the overlord and his attached bachelor or between either of these and any male of the colony, irrespective of age, with whom temporary friendly relations are assumed. The beginning of such relations is usually manifested by quick lip, jaw, and tongue movements (usually described as smacking of the lips), such as occur during the process of grooming. These tongue and lip movements form an essential part of all friendly and sexual activities, both as a preliminary gesture and as an accompaniment. Two animals will be sitting near each other, their heads will turn, their eyes meet, and immediately they may begin to smack their lips. This social response may then be extended by the animals rising, and by one presenting to the other. Then follows more pronounced smacking of the lips, sometimes a rhythmical series of low deep grunts, and the animals will either groom each other or mount each other, or do both. The females of a harem also exhibit homosexual behaviour—one female assuming the attitude of the male in mounting another. Since the females of different harems do not come into contact with each other, feminine homosexual behaviour occurs only in harems containing more than one female. Females also assume the male position and mount young males, and on rare occasions adult females have been observed mounting bachelors attached to their harems.

Female baboons on Monkey Hill may sometimes be seen examining their ano-genital regions with their fingers, but they have not been observed actually masturbating.* The habit is commonly practised by all the males of the colony, including those that are mated. An animal thus engaged does not appear to stimulate the interest of neighbouring baboons, nor does mutual masturbation occur. It is difficult to decide whether or not this form of behaviour is

* Isolated females in cages occasionally masturbate.

elicited by the unnatural environment of captivity. As already mentioned, according to Marais it is a natural response that may be observed among wild baboons.

CHAPTER XV

DOMINANCE AND THE LIBERATION OF SEXUAL RESPONSES

THE sexual responses of sub-human primates may have no connection with sexual appetite, and often appear to be used as a means to obtain material advantages,—for example, food or protection from enemies. The liberation of these responses in asexual situations was first recognized as a distinct form of behaviour by Hamilton in 1914.[136] Hamilton concluded, from a lengthy series of observations, that "at least two, and possibly three, different kinds of hunger, or needs of individual satisfaction, normally impel the macaque towards the manifestation of sexual behavior, viz., hunger for sexual satisfaction, hunger for escape from danger and, possibly, hunger for access to an enemy." To this list Bingham, on the basis of certain observations carried out in Cuba on the late Madame Abreu's collection of sub-human primates, has suggested the addition of a fourth class of sexual responses—the tendency "to show off sexually in the presence of interested observers."[40]

In an earlier chapter it was stated that the liberation of sexual responses from the function of reproduction may be regarded anthropomorphically as sexual prostitution. This point of view is emphasized by Kempf,[211] who defines the prostitution of the sub-human primate as being "essentially the giving of sexual favors for economic advantages and physical protection." The strong teleological bias of this interpretation has drawn the criticism of Bingham who maintains that it "implies too much in the direction of ideational equipment and thought processes. The

bartering attributed to the monkeys presupposes an appreciation of relative values to an extent that I am not prepared to concede even in the chimpanzee." At the same time Bingham admits that the anthropomorphic view is a quite natural outcome of data that relate only to perfected social responses. As he rightly points out, if the developmental phases of the fully formed social responses classed as sexual prostitution were known, the perfected behaviour that implies insight might be seen to be simply conditioned responses. He himself has shown that the sexual presentations of his chimpanzees at times when they were fed had "unmistakable roots" in previously exhibited behaviour connected with fear and rage.

The distinction implied by Bingham between prostitution that is accompanied by insight and prostitution that may be a conditioned response is perhaps not altogether justifiable. Prostitution is not the interpretation of the processes underlying the relevant responses—it is the interpretation of the actual results of the behaviour. Thus if a particular response of a sexual nature is always followed by the acquisition of some social or material advantage, it is legitimate, for purposes of description, to refer to the response as a form of sexual prostitution, whatever its history. The extent to which these forms of response are innate or socially conditioned in monkeys is altogether unknown, for in spite of their obvious importance, no complete studies of their development have as yet been made. My own observations suggest that they are in greater part socially conditioned forms of behaviour, and that they are mainly an effect of the system of dominance upon which sub-human primate societies are based. The permanent bi-sexual associations of monkeys and apes form an adequate environment in which the complex sensori-motor equipments of these animals may evolve new types of social and sexual response.

Every ape or monkey enjoys a position within a social group that is determined by the inter-relation of its own

dominant characteristics and those of its fellows. The degree of its dominance determines how far its bodily appetites will be satisfied. Dominance determines the number of females that a male may possess, and except on occasions when there is a superfluity of food, it also determines the amount a monkey eats. Sexual prostitution can be regarded—indeed this is the only possible interpretation in the light of the facts at present available—as a means by which monkeys survive within a social framework that achieves a dynamic character by a system of dominance. In many cases the assumption of the female sexual attitude by one animal towards another, implies that in this situation the "presenting" animal is submissive to the other.

Social relationships based upon dominance occur throughout the animal world. Rutting seals secure that piece of territory in the breeding ground allowed them by their order of dominance within the group. The dominance of a stag determines the number of females he includes in his harem during a mating season. Monkeys and apes are therefore not peculiar in this respect. Their dominant relationships, however, are conspicuous because they characterize every field of behaviour. If a group of monkeys finds itself in a feeding ground in which there is an abundance of food, every animal will be able to eat. If, on the other hand, food is passed into a cage containing two or more monkeys, the strongest animals will secure all. As a rule the weaker animal will not even attempt to obtain any food. If by any chance it does and is also unfortunate enough to attract the notice of a more dominant animal,—who at that moment does not happen to have its mouth and cheek pouches full,—in all probability it will be attacked. If it does not disgorge the food contained in its cheek pouches, they will be raided by the exploring fingers of the dominant animal. For this reason a great deal of care has to be taken in the selection of monkeys that live together in a single cage. When the dominance of a few animals is

very pronounced, the weaker members in a cage would starve if it were not for the protection they get from keepers. Owing to shortage of accommodation it was once necessary to confine seven Rhesus monkeys and a common macaque in one cage in the London Zoological Gardens. When food was passed in, four of the animals, who were completely dominated by the others, would immediately climb to the wire forming the roof of the cage, where they clung while the more dominant animals fed. After a certain interval a keeper would drive these four from the floor of the cage and, as they climbed up, the other four descended, the keeper remaining on guard while these weaker animals fed.

Dominant relationships also prevail among the members of a family. If a limited quantity of fruit is thrown to a male sitting with his female or females he will eat all. Six bananas, one after the other, were thrown to a pair of baboons—the one a male, the other his female who was nursing a newly-born baby. The male snatched them all, keeping those he could not push into his cheek pouches in a heap in front of him, while his female made no attempt to secure any. As was mentioned in the previous chapter, she might have obtained some had her sexual skin been swollen. Domination also extends to other material objects. A small baboon picks up a basket or a glove that has been thrown on to the Hill by a visitor. An adult male approaches, the young animal squeals and rushes off, dropping the basket or glove, which may be picked up by the mature animal. Fundamentally, females are also treated as material objects, and are secured by the more dominant animals, the weaker males remaining unmated. In a baboon colony an animal may be dominant so far as females are concerned, whereas his dominance may not be exhibited at feeding times. An overlord may scuffle with bachelors for the possession of some fruit and may be worsted. He does not, however, thus lose caste, nor do such circumstances usually lead to serious fighting. If, on the other hand,

adult bachelors were to try to steal his female, the situation would immediately result in serious fighting. If the bachelors are routed in such a fight, the overlord maintains his dominant position within the herd. If, on the other hand, he is dispossessed, he immediately loses caste, to become submissive to those animals whom he formerly dominated.

Domination also extends into the sphere of punishment, since monkeys and apes usually "hand down" the punishment they receive. For example, it was once necessary to examine daily an adult female Abyssinian cercopitheque who lived in a cage in the London Gardens with a small South American woolly monkey. In order to do this she had to be taken out of the cage, a form of treatment she greatly resented. When the examination was over and she was returned to the cage, she invariably signalled her liberation by an immediate attack upon the weak woolly monkey. Domination also characterizes the sphere of friendly relations. A small adult female Hamadryas baboon living alone in a cage of the Monkey House in the London Gardens always came to the wire to be stroked and groomed by several human "friends". An immature yellow baboon which was bigger than the Hamadryas female was introduced into the cage. At first the Hamadryas attempted to dominate her in all the activities of the cage. After a while the position was reversed, and the bigger yellow baboon began to torment the Hamadryas. Within a few days the Hamadryas baboon refused to come down to be stroked and petted, maintaining a passive attitude as if she were unaware of the inviting fingers beckoning to her through the wire. This behaviour continued throughout the period the yellow baboon remained with her, but as soon as it was removed she immediately resumed her former habits. The assistance one monkey gives a tormented fellow frequently depends upon their relative positions in the scale of dominance. A bachelor mature baboon threatens an immature male on the

Hill. The young animal squeals in terror and immediately attracts a more dominant adult, who begins to threaten its tormentor. Substitute female for immature male, and this description becomes typical of relationships within a harem, the overlord being the dominant protector.

Female baboons are always dominated by their males, and in many situations the attitude of a female is one of extreme passivity. For example, she behaves as though paralysed when males are struggling for her. The subjugation of the female sub-human primate forms one of the main distinctions between the harem of the monkey and the harem of the lower mammal. It is the female lower mammal who allows or does not allow mating, but it is the male primate who mainly determines the time and frequency of coitus—though his behaviour is, of course, stimulated by the physiological condition of the female. Female baboons are passive both in the matter of their disposal and in their usage as sexual objects.

Social relationships based upon dominance may be regarded as a series of adapted responses conditioned through pain and fear. The scope of an animal's activities within a group will be limited by the possibility of danger arising from its desires overlapping those of a more dominant animal. The only equality within a social group is an equality of dominant characteristics. A state of balance is only temporary, and at any moment may be disturbed to a greater or lesser extent, the members of the group readjusting their mutual relationships. The group then settles down in a new equilibrium. Within a group each animal seems to live in potential fear lest another animal stronger than itself will inhibit its activities. A dominant monkey will take all the food passed into the cage, but will start in a momentarily terrified way when one of its weaker fellows, in moving some object, makes an unusual noise. An inferior animal will move towards some food that is proffered, stop suddenly, turn to look at its

dominant companion, and then retreat, making those noises that are associated with situations of fear and submission.

Both the male and the female primate are always to some degree in a sexually excitable condition, and the stimuli that can release their sexual responses are enormously varied. Any member of a social group, old or young, will stimulate sexual responses in another. A monkey will, as Hamilton has shown, also attempt to use kittens, puppies, foxes, and even snakes as sexual objects. Baboons chained up to stakes on farms in South Africa are often observed proffering themselves sexually to dogs. All kinds of objects may be used for sexual purposes. A female ape will masturbate with fruit, glass and sticks. This diffuse sexuality allows sexual behaviour to become conditioned and adapted to the rigours of a social life that is based upon a system of dominance. The lack of definition of socio-sexual responses, the variety of the forms they take, and the numerous situations in which they are released, provide adequate scope for their "prostitution" or modification.

All situations which stimulate sexual prostitution are alike in so far as they allow an animal some advantage that it would otherwise be denied. A weaker animal secures some food and immediately presents sexually to a more dominant fellow. Its act of sexual submission may or may not be followed by the dominant animal mounting it or grooming it, but the sexual stimulus usually serves as a means of inhibiting the dominant animal's initial response of antagonism aroused by its deprivation of food. In this connection one is reminded of Lashley's remarks on the impulsive character of the behaviour of terns [227]—"One group of stimuli seems to gain momentary control and determine the bird's reaction in spite of contradictory elements in the situation as a whole." A strange chick that at one moment is defended by an adult from the attacks of other birds of the colony is at the next attacked by its former protector. "The sight of the strange chick calls out

movements of attack; the sight of an adult attacking a chick calls for defense of the chick." A similar conflict of stimuli occurs when the attacked chick forces its way under the body of the aggressive adult, thus inhibiting the aggression and stimulating a brooding response. If the adult bird is at some distance from its nest, its attitude soon reverts to one of aggression.

The behaviour of the terns affords a close parallel to the behaviour of baboons or of other monkeys in situations of sexual prostitution. The transition of the aggressive reaction to one of brooding is the same in kind as the transition of the aggressive attitude of a monkey to one of sexual interest when it is presented with a sexual stimulus by the animal whose activities have aroused its aggression. From the analytical point of view the overriding nature of the sexual stimulus is more important than any knowledge of the genetic background of such responses as come under the heading of sexual prostitution. However it is possible that these liberated sexual responses are socially conditioned from flight reactions stimulated by fear.[40] This view implies that the acts of sexual presentation of a monkey—other than those directed to sexual ends, whether reproductive or playful in nature—represent incipient flight responses in situations in which the animal is dominated. The monkey's presentation in social situations of this nature is then all that is left of its original reaction of flight from the environment of fear and discomfort. The act typifying subjugation accordingly becomes the movement of turning and the presentation of the hindquarters. The inhibition of flight may be regarded as an effect of social conditioning, since the turning of the hindquarters at the beginning of the reaction presents a dominating animal with a sexual stimulus to which he immediately responds. This new stimulus is stronger than the one that has evoked the display of his aggression. Such a series of events could possibly form the background out of which develop the modified types of sexual

response which characterize an animal's adaptation to a social life ruled by dominance.

An instance of a weaker animal obtaining food in the presence of a dominant fellow was quoted as an example of sexual prostitution at the beginning of a preceding paragraph. In the place of food any material object might be retained in the same way by the weaker animal. By proffering itself sexually it might also ward off a threatened attack. A young animal draws the threats of an adult. It may then immediately rush away or alternatively present, usually squealing at the same time, the change in its behaviour thus inhibiting the threatened attack. The two animals then pay no more attention to each other, or alternatively the young animal approaches the dominant one in the sexual position and is immediately embraced, perhaps groomed and even mounted. Sometimes one observes an animal that is being tormented by another run to it and clasp it tightly in an embrace. The screams of an animal presenting to a tormentor may attract another animal, who rushes forward as the dominated animal's protector, covers it and threatens the one that was tormenting it. An animal may present sexually in order to attract an enemy. Though this form of prostitution is not commonly observed on the Hill, it is often manifested by caged animals. A monkey on one side of a wire-netting may often be seen pressing some part of its body to the mesh to be groomed by one of the animals in an adjoining cage. When the stimulus draws a response, the animal that has proffered itself suddenly snaps at the fingers that have been pushed through the wire. A human observer may also participate in such a situation and begin to pick an animal that has presented through the wire. Suddenly the animal turns and attempts to bite. Other circumstances may also be observed in which a sexual approach is used to obtain access to an enemy. For example, a young male monkey playing with an immature female of about the same size moves as though it were about to mount the female

sexually. As she responds, and in presenting turns her back, the male immediately bites her. Such behaviour may be repeated time after time, perhaps partly in play, within the space of ten minutes. A common form of behaviour to be observed on the Hill is a sexual approach that seems to precede the enlistment of allies before a scuffle takes place. One baboon approaches another, smacks its lips, presents, and, having evoked a reciprocal response from the other animal, immediately turns round and threatens, by gesture, some animal who, previous to this performance, did not seem to be in any way involved in the situation. Its threatening attitude is immediately reflected in its new friend's behaviour, and both become aggressive towards the third animal. This type of "sexual prostitution" may be regarded anthropomorphically as a means of securing an ally. It seems to bear some resemblance to another form of behaviour exhibited by younger animals in their play. Two will be playing when one suddenly stops and moves off. Its fellow may then immediately assume the copulatory position, looking backward at its retreating playmate. When meeting, baboons on the Hill may pay no attention to each other's presence: they may show pugnacity, and threaten each other: or, on the other hand, they may make friendly advances, smacking their lips, the while one presents to the other. Thus a sexual approach can usually be interpreted as a friendly greeting and a sign of good feeling.

Modified sexual responses are often manifested within the sphere of the harem. Any animal may lead in the movements of a family party, but occasionally when a female attempts to lead she may not be followed by her overlord and the rest of her group. On such occasions the female, after looking round at her stationary companions, returns and presents persistently to her overlord, and at the same time she may squeal continuously. Her behaviour usually stimulates one of two characteristic modes of response. He may either attack her or, on the other hand, he may be

attracted as she moves forward in an attitude of presentation, and as he follows her, he is in turn followed by the rest of the party. The customary presentation of a female to her overlord after she has been unfaithful has already been noted. This may occur whether the male with whom she has had sexual contact is an adult or an immature animal.

When the five females were removed from the Hill and isolated with an adult male, as explained on page 219, they formed a harem that provided excellent opportunity for study of the detailed responses of the individuals within such a group. Previously on the Hill, and again in their new environment, the adult females displayed temperamental differences that were best recognized by comparing their behaviour in corresponding sexual phases. It was obvious that they had a scale of dominance. Some asserted themselves more than others, particularly at feeding times, when the more aggressive animals attempted to obtain more from limited supplies of food. Their degrees of dominance were also manifested in their fear reactions to the overlord, and could be seen in their varying degrees of aggressiveness to the human observer. One female in particular seemed to resent close observation, and regularly threatened the onlooker. Sometimes she would present to her overlord, regarding him fixedly and squealing as though she had been threatened.* Her behaviour often stimulated his aggressive responses towards the observer.

The male who was chosen to accompany the five females banished from the Hill was the overlord of the immature female who had been born in October of 1928. He had taken charge of this animal about a year before their removal to their new quarters, and the two were well adjusted to each other in their general, though not in their sexual, behaviour. The little female dominated the four adult females for about three

* These animals were not on exhibition for several months and had become somewhat unused to being observed.

weeks, showing her superiority by her lack of fear and the readiness with which she came to the front of the cage to receive fruit that was offered. At the beginning she did this without looking round to observe the reactions of her overlord, her assertiveness representing the only conspicuous difference between her attitude and that of the adult females towards the male who dominated them all.

No mating behaviour was observed during the first week after the formation of the harem, all the adult females then being in a quiescent phase of the sexual skin. During this time the male's previously established relationship with the young female did not appear to be affected. He still seemed to favour her more than the others, even though they often groomed him and presented to him sexually. The first significant change in his general demeanour was noticed about the eighth day, at a time when each of the four adult females was at the beginning of a phase of sexual-skin swelling. He was then observed mating with the female who was most assertive in her heterosexual advances and in her assumption of the masculine rôle in homosexual activities with the other females. A few days later, when all four females were showing a maximum amount of swelling, the male became irritable, attacking his females as they persistently presented. At this time he continued to pay no attention to the immature female's acceptance of food that had been passed into the cage. On the other hand he viciously attacked one of the sexually attractive adults who was doing the same, and during this period of irritability he killed the baby she was nursing.* The swelling of the sexual skin of this female persisted longer than that of the others, and by his behaviour it was obvious that he found her the most stimulating sexually. In addition to mating with her, he often followed her round the cage, biting her, usually in the scruff of the neck. These "attacks" were carried out without any noise

* See below.

from either animal, and they did not seem to interest the other females in the cage. A significant change then appeared in his relations with the young female, who no longer descended fearlessly to accept fruit in the face of his threatened attacks. Whenever she had gathered the necessary courage to take an offering, she presented squealing in terror to the now antagonistic male and often dropped the fruit she had just accepted. A change also appeared in his social adjustments with the adult females of the harem. From this time most of his attention was occupied by any female who, at the time, was showing the greatest swelling,* the favoured position of this female being shown, for example, by her readiness to accept offerings of food.

As they became socially adjusted, the "temperamental" differences between the four females became increasingly obvious. They formed temporary friendships amongst themselves. This is noteworthy, since none of these females had had any experience of each other's company for at least two years. One of them was especially masculine in her reactions, mounting her fellow females more than they did one another. She also showed a greater regard for the movements of the overlord during all her sexual phases, and became very aggressive towards observers. As has been noted, this female often made the male participate in her hostility by presentation and by squealing. A second female, who in many ways was in better condition than her fellows, became the most independent member of the cage. When introduced to the new harem she was nursing a six-months-old baby that was subsequently killed by the overlord. She showed signs of her independence at a very early stage by attempting to secure food. At first she was very tentative in her movements and seldom approached the wire without simultaneously presenting,

* Although the four females were approximately in the same reproductive phase at the time that they were put together, their phases of sexual-skin swelling rarely coincided subsequently, owing to differences in the lengths of their menstrual cycles.

but after the death of her baby her independence became more pronounced. The third female was a somewhat passive animal who, after the first few days in the new environment, kept closest to the most subdued of the four adult females. This third female very rarely attempted to obtain food offered to her, and maintained a persistently passive attitude except in her phases of sexual-skin swelling, when she naturally assumed the position of chief female in the harem. The fourth female had been previously owned by the bigamous male on Monkey Hill. She was very subdued in all her movements, even during her most active sexual-skin phases. At times she rarely made a movement without first regarding the position of the overlord to whom she persistently presented. She appeared to be in a constant state of subdued terror. So far as I know no serious attack had been made upon her by her new overlord to account for her behaviour.

The circumstances of the death of the baby that was being nursed by the "temperamentally" independent female are worthy of record. It was four and a half months old when it was removed from the company of its father and taken with its mother to the cage in which the new harem was formed. At that time its movements were sufficiently well co-ordinated for it to leap a gap of eighteen inches. With the exception of the overlord, all the animals in the cage were at one time or another observed attending to it, examining its genitalia, attempting to groom it, and embracing it. The young female in particular was often seen playing with it. The first attack made upon the baby by the overlord was noticed on an occasion when the mother was attempting to secure some food that had been thrown into the cage. The moment she had picked up a piece of fruit she presented to the male, who, nevertheless, immediately assumed a threatening attitude towards her. The female thereupon dropped the fruit, only to pick it up a second time about a minute later. Again she presented, and this time the male

sprang upon her and bit her in the back. The baby was moving close beside her at the time of this attack, and immediately afterwards it climbed upon her back. Undeterred by the assault, the female again attempted to secure some of the food. The male once more launched an attack upon her, bit her in the scruff of the neck, and this time suddenly transferred his attention to the young animal riding on her back, biting it viciously in the loins. The baby was thrown to the ground and was immediately gathered up and carefully nursed by its mother, while the overlord retired to a corner of the cage. A similar assault upon the mother and baby occurred about a quarter of an hour later. The baby was found dead that evening.

Variability in the behaviour of females such as has been discussed in the preceding paragraphs, may be called "temperamental" in the absence of knowledge regarding its basis. Temperamental changes that are probably correlated with physiological mechanisms may be observed in the attitude of a female baboon towards the close of gestation. She then becomes more subdued than she is normally. Her general activity is diminished, and she spends the greater part of the day quietly sitting beside her overlord. In monogamous parties the diminished activity of the pregnant female affects the movements of the male, and both animals appear very quiet.

The behaviour of the bachelors that attach themselves to family parties presents many points of interest. It has already been mentioned that certain family parties attract bachelors more than do others, and it has also been noted that the bond holding the bachelor to the family party is probably his interest in the females. This is indicated by the fact that the bachelor of a monogamous family party does not continue to associate with an overlord after the death or removal of the female. One bachelor who had been attached to a monogamous family continuously for one year, and intermittently for two years, almost entirely ceased to consort with its

overlord after the female had been removed from the Hill. Instances of infidelity between females and bachelors attached to their harem also lend support to the view that the bachelor is held to the group mainly by his heterosexual tendencies. Attached bachelors sometimes exhibit their sexual interest in a peculiar way. When the overlord initiates a change in the family party's position, his female or one of his females may be slow in responding. The bachelor may then stare persistently at the female's eyes, alternating this gaze with a searching look at the overlord, who may be looking back at his lingering female. After a little while she follows. On the disruption of a family to which they have belonged, some bachelors have evinced an occasional interest in other family parties. There have been other unmated males, however, whose attraction may have been more specific, since after leaving a harem to which they had been attached for a period, they have never again joined either the same or any other family group. The part played by an attached bachelor in a "sexual fight" that leads to the disruption of a harem is discussed in the following chapter.

CHAPTER XVI

THE COMMUNAL LIFE OF THE BABOON

THE behaviour of the members of a baboon harem has been discussed in preceding chapters, and one may now consider the wider social environment within which the harem exists. On Monkey Hill in the London Zoological Gardens unmated males, or bachelors, form the most important element in the social background of the family group; whereas in the "Affenland" in the Tierpark near Munich the greater part of the population consisted in 1929 of immature males.

The sexual and social behaviour of the bachelors is identical with that of the mated males of the colony, except for the absence of overt heterosexual responses. Most of the unmated males on the Hill usually wander about and sit alone, except for those periods when they are engaged in sexual or grooming activities with a fellow. The smacking of the lips and presentation, which usually initiate their friendly relations, have been described in Chapter XIV. Lip movements also accompany the actions of a bachelor who touches the genitalia of another as he passes—this gesture sometimes leading either to grooming or to other homosexual responses. Bachelors occasionally strike up "friendships" with each other, and for a time a pair of animals may be seen constantly together. Friendships also exist between an older male and a younger male. One such relationship lasted three years, and was ended recently by the death of the younger baboon, who at the time of death was adolescent. This young male was seldom seen to mix with the other immature animals of the Hill. Whenever it was tormented and

squealed, it was immediately rescued by its protector, with whom it often engaged in homosexual activities. The relationships that existed between bachelors and the young female born on the Hill were perhaps of a different order, since they always had a heterosexual basis. They are discussed at a later stage, when the development of the young female is considered. It is perhaps interesting to note here that when all the females were removed from the Hill, the abandoned overlords immediately merged with the group of bachelors. An observer with no previous experience of the colony would be unable to pick them out to-day.

Rarely a day passes without a scuffle between bachelors, but it is often difficult to understand the causes of their quarrels. Occasionally it is due to a baboon attempting to secure food that is snatched by a more dominant fellow. Sometimes a fight is precipitated by one animal rushing to attack another who has evoked a squeal of terror from an immature animal. Usually, however, fights are begun as a display of dominance, one animal suddenly threatening any other in its vicinity. The aggressive baboon begins to grind its teeth, to "yawn"*, to grimace and stare at the enemy it has chosen, while it makes quick thrusting movements on the rocks with its hand. The response to such behaviour is almost reflex in character. The threatened animal, either alone or together with its neighbours, begins a reciprocal display of dominance. Once two are involved in such a quarrel, it is rare for others not to participate. They rush to the scene, generally joining the animal who is at the moment less dominant. Sometimes the disturbance spreads throughout the colony and mated males and their family parties join in the fight. The more aggressive animal seems to be unaffected by the increase in the number of the

* This gesture is performed by many monkeys and shows little variation. The yawning threat of the Gelada baboon is accompanied by complete eversion of the upper lip, which flaps back as the animal opens its mouth.

enemies he has called upon himself, and thus the baboon fight assumes its peculiar character—a single animal defending himself against a group. The sexual presentation which sometimes accompanies the enlistment of allies in these fights has already been described. At other times animals are attracted by the cries and attitude of the dominated baboon, continuing throughout the course of the fight to regard one another's movements closely. It is rare for these scuffles to develop into fights in which the animals seriously hurt one another, the aggressive animal usually routing the group he opposes. Every time he darts forward they retreat. As he retreats they advance, the wounds that are made being inflicted during these sudden dashes. During the scuffle, two of the animals belonging to the group that has collected to oppose the aggressive animal may suddenly begin to fight each other. Their activities soon attract the attention of other participants in the general fight, which may then immediately "change front". Thus, one usually notices that the central figure of the scuffle—the animal that has been opposing the group—suddenly changes places with one of his opponents, and joins with them in threatening an animal who, a moment before, was one of their allies. Such a series of events may be repeated several times during the course of a lengthy fight.

Overlords of harems engage in fights for many reasons. They may be attracted to the scene of a quarrel already in progress, their behaviour on such occasions not differing essentially from that of the unmated males. On those occasions when the overlord does not take a leading part in the fight, and has not attracted the attention of the other participants, his female or females often show fight and accompany him in his movements in the scuffling group. At other times the females may remain on its outskirts. His behaviour differs when he becomes the central figure of the fight, a situation of this kind arising in a variety of ways. In a display of dominance he may threaten,

PLATE XIX

Photograph by J E Saunders

THE BABY BABOON'S MOVEMENTS CONTROLLED BY ITS MOTHER

A young male in left foreground (See p 260)

pursue and rout either one or several of his fellows without actually inflicting wounds, and without any signs of retaliation on their part. On such occasions the members of his harem generally follow his movements. At other times his aggressive activities may be aroused by his perception of the "fear-threatening" attitude of one of his females or of some other animal. Mention has already been made of this behaviour in connection with the submissive return of a female after she has had promiscuous contact with a bachelor. The characteristic squeal of a terrified animal as it threatens another usually evokes an immediate response of aggressive protection from any neighbouring dominant animal. It is unnecessary to assume, therefore, that an overlord who responds to the "fear-threatening" attitude of one of his females has any ideational apprehension of the fact that it is his female rather than any other animal who is behaving as if it were being attacked. Sometimes an overlord may suddenly draw the aggression of his neighbours for no obvious reason. Since this occasionally happens at feeding time, when all the animals are crowded together, it is possible that the animals have quarrelled over food. At such times, and at others when the overlord has evoked the combative activities of his fellows, his female or females usually and immediately assume a copulatory position and crowd around him—in a monogamous party the male mounting his female as he threatens his attackers. A bachelor attached to a family party was once observed covering a female in this way while the overlord took a more active part in a fight. If other family parties are in the vicinity of these scuffles, their members behave in a similar manner, or immediately move away to a quieter area. Every family on the London Hill was attacked at some time or other, but usually the contests proved abortive, the overlord succeeding in routing his enemies. Since no observation has been made of an overlord seeing his female in sexual contact with another adult male,

it is unknown whether or not these abortive fights ever represent the outcome of his reaction to her infidelity. It is possible that they sometimes represent an attack by unmated males who are trying to obtain a female of the harem. Unfortunately, no fights have been observed intermediate in severity between abortive scuffles which are usually of short duration and the serious "sexual fights" that are described in the following paragraphs.

The normal behaviour of most unmated male baboons suggests their passive indifference to the presence of females within the colony. On rare occasions, however, the atmosphere suddenly changes and every male appears to be trying, at the peril of life, to secure a female in an attack upon a harem. The behaviour of one male influences another, and there have been few "sexual fights" on Monkey Hill in which most members of the colony have not been engaged. Though mated animals have never been known to initiate a "sexual fight", almost all of them have been observed participating once such a fight has begun. The "sexual fights" on Monkey Hill have been so serious that they have been responsible for the deaths of thirty female baboons. After each of the serious fights had ended in the death of the female round which it raged, the colony settled down in a state of balance which, as subsequent events proved, contained all the seeds of further disruption.

Signs of the decreasing dominance of an overlord were sometimes noticed some months before an attack was made upon him. For example, the last female to be killed on Monkey Hill had been lost by her overlord for a short time three months previous to her death. The beginnings of social disruption were at times also presaged in other less obvious ways. Thus each of the three "sexual fights", most of whose phases I myself observed, were preceded by subtle but significant changes in the social relations of the overlords who were subsequently attacked. They seemed to be avoiding contact with their fellows, in whose attitude the

observer could detect a growing aggression. The sexual condition of the female is apparently in no way connected with the outbreak of hostilities. The females who have been killed have represented all phases of the reproductive cycle. Some have died in a phase of swelling of the sexual skin, others in a quiescent phase of the skin, and one animal was pregnant at the time of her death.

I have not observed the actual beginning of a "sexual fight", but observations of their general course indicate that it starts in the same way as all other fights—as a quarrel between two animals. There is no evidence that it begins as a concerted attack of unmated males upon the harem. The "sexual contests" seem to follow a stereotyped course, and the only significant differences that have been observed have been those between fights involving a monogamous family party and the fight that concerned the bigamous harem. The initiator of one fight was the bachelor who until then had been attached to the family party and the following description is based mainly upon the behaviour observed in this fight.

Some time before the beginning of the fight a change was noticed in the behaviour of this bachelor. He always kept near to the single female of the party, but at the same time appeared to be regarding the movements of the overlord even more closely than usual. When the party was on the move he would repeatedly hang behind with the female when she lagged. At this time no change was observed in the behaviour of the overlord. Five days before serious fighting broke out, the bachelor was observed threatening the overlord, who turned on him and routed him without coming to blows. No other animals were in the neighbourhood when this attack occurred. Five days later fighting broke out and the female was seized by the bachelor, the two animals and the overlord forming a single party upon which was focussed the aggressive attention of all the other combatants. It was the

bachelor, however, who persistently covered the female with his body so that she was unable to move. Her attitude seemed completely passive as she was pulled from place to place by her new owner, who groomed her fur and occasionally mounted her. Although the overlord was in their immediate vicinity, he did not appear to be paying any attention to their new relationship. He was far more interested in the bachelors and family groups who were crowding round and threatening his party. Every now and then he rushed at them, and they instantly scattered. The surprising feature of this phase of the "sexual fight" was the apparent indifference of the overlord to the fact that the bachelor was in possession of his female. On the following day, however, he regained his female, only to lose her for a second time to the same bachelor within twenty-four hours. The capture and recapture of this female by other bachelors was observed on several occasions, occurring usually in the midst of a general scuffle. As the three closely observed fights have shown, a female may change hands several times before the fight has ended.

During such a fight numerous scuffles over the body of the female may occur in the course of a week. During the quiet intervals she may be observed, much the worse for wear, grooming or being groomed by her seducer. As soon as other males approach, he stands over her crouching body and threatens his attackers by dominantly displaying his teeth. This gesture, which is repeated and alternates with gnashing of the teeth, may ward off the interested animals for a while. But suddenly they attack. There is no concerted action or strategy about their movements. The female's body remains covered by the male who has her for the moment, while he defends himself from the assaults of the crowd of males. Hands will be seen trying to pull the prized female from under his body, but so far as is possible he keeps his position. Every animal bites every other in any part of the body that is

exposed. Such a general scrimmage seldom lasts more than a minute or two, when the attackers retire. During the mêlée the sought after female has remained completely passive, making no attempt to retaliate or to ward off bites. Her passivity continues after the fight, and she does not resist when she finds herself in the hands of a new male. Usually a male who succeeds in obtaining the female manages to hold her for more than one attack. Between successive storms he may move to a more strategic position. Favourite places on Monkey Hill have been against a wall of rock or down a well in front of one of the entrances to the sleeping dens.

The Hill is seething with excitement after a "sexual fight" has been in progress for a day or two. Small isolated fights take place between the bachelors. When a bachelor settles for a moment he looks round, regarding the attitudes of the animals near him, frequently threatening them all by facial grimaces, by opening his mouth and displaying his teeth, which he continuously grinds, and by quick thrusts of his hand. Every now and then he rushes at his neighbours, who immediately retreat. By human standards baboons are very cowardly animals, since a single one may, by what seems to be a vain display of dominance, vanquish a group of his fellows. When the members of one harem join in the attack on another, the females behave in the same way as they do in less serious fights. Sometimes with their overlords they aggressively join the fighting animals; at other times, when an overlord is on the defensive, he may cover the body of his female as he threatens the animals whose attentions he has drawn from the centre of the fight.

A "sexual fight" usually results in the death of the female over whom it has raged. While it is in progress she suffers continuous physical torment, and may also be unable to obtain food. She is mounted by every male who succeeds in winning her. The fight continues over her dead body, and the males still treat

her, even though dead, as a sexual object. As the dead body was always removed as soon as possible from the Hill, it was impossible to discover what the natural end to a "sexual fight" would have been.

The attitude of the overlord directly concerned in the fight usually varies in the successive stages of the battle. Mention has already been made of the apparent indifference of an overlord to the seduction of his female by a bachelor who had been attached to his family party. This may have been partly due to the fact that by the time of the fight, he was so conditioned to the bachelor that he continued to perceive him as a normal companion of his female. In the later stages of the fight the overlord becomes one of the group of attackers, and when finally vanquished he joins the body of bachelors. In one case an overlord became the companion of a bachelor who dominated him completely, following this animal wherever it led. When he was slow in following, the bachelor would turn and regard him fixedly until he moved.

Sporadic fighting may continue for a while after the removal of the body of the dead female. In spite of the serious wounds that many received, no animals other than the coveted female were killed in the fights that were witnessed. There were a few bachelors on the Hill who remained apparently unperturbed when the colony was in a state of disruption, and who were not observed taking part in "sexual fights". Usually the less pugnacious of the mated males also withheld from the fights. The attentions of the bachelors engaged in a "sexual fight" are so focussed upon the female who is its centre that they do not divert the attack on to one of the females who has followed her overlord into the fray. Perhaps this is partly due to the fact that in fighting these aggressive females play a somewhat masculine part. They do not adopt the passive attitude of the coveted female.

The last "sexual fight" that took place on Monkey Hill was peculiar in certain respects and involved the

harem containing two females. It had been obvious for some time that the overlord of this family party was declining in dominance. For several days before the fight broke out both of his females showed a maximum amount of swelling of the sexual skin, and both appeared to be in a highly sexual state. They persistently presented to their overlord in a crouching position, and in response to their gestures he sometimes mounted them, at other times groomed them, and often attacked them viciously, concentrating his bites on their backs. The first seducer in the contest that followed was a rather powerful unmated male. The fight was peculiar in so far as the overlord ignored his female after her initial seduction and took no further part in the fight. He walked about with his remaining mate and never turned his head when passing the scuffling groups that covered his other female. At times he was seen attacking the female left to him, pulling her down and biting her whenever she moved. The fight lasted for several days and after the female was killed, twenty-four hours passed before the body could be removed from the Hill. During this interval fights continued to rage round the body, which changed hands several times. Its owners carried it around by the waist, groomed it, examined its ano-genital area, and often copulated with it.

Although their squeals of terror may precipitate a fight, the immature baboons in the colony usually move unmolested through groups of scuffling adults. The cry which draws the protection of a mature animal may be given in a variety of situations. It may be evoked when the young animal is bullied or threatened by a mature baboon. At other times the immature animal may have been hurt in a fight that started in play with a fellow of its own age. Most commonly, however, a young animal is heard giving a squeal of terror for no reason that is obvious to the human observer. Some adults rush to the scene, threatening one another, and the young animal scampers away.

Immature baboons are much more active than the mature animals, and are usually seen playing. No permanent "friendships" were observed amongst the young baboons in the London colony, and observations were not made over a sufficiently long period to determine whether or not they existed in the Munich "Affenland". Mention has already been made of an immature baboon that was permanently attached to an adult male on the Hill.

The play activities of the young animals are varied and numerous. They are often to be seen fighting and tumbling with one another. A crippled adult male was once observed being tormented by two immature males, who were then set upon by another immature animal bigger than themselves. The adult made off and the young animals continued to tumble and fight with each other. On another occasion a young male was playing roughly with a small four months old baby belonging to a harem. The baby screamed and its playmate hastily escaped.

The young animals are attracted by all kinds of objects, and can be seen playing with whatever happens to be thrown into their enclosure. They will carry bags in their hands and wear baskets on their heads. They tinker with the remains of watches thrown them by generous visitors, and carry pipes in their mouths. In Munich they can often be seen playing with toads that they have dug out of the wet earth. I once observed a group of young baboons holding a toad they had brought in with them into their sleeping quarters, and closely examining its movements. In play one young animal may carry another, who rides like a jockey on its back, or hangs from its belly in the way that a baby is carried by an adult female.

Sometimes a young male attaches itself to a harem. One in particular was often seen in the company of the same female, whom he frequently mounted. They often join bachelors, with whom they engage in mutual grooming and sexual activities. The older animal

folds its young friend in its arms, as an overlord does his female, and a mother her infant. An overlord may embrace a young animal in this way even when his females are in the immediate vicinity.

A young baboon is often covered and groomed by an adult animal, whose threatened attack has stimulated it to present. Adult males have sometimes been observed covering young animals who attempted to escape. Sometimes the terrified squeal of a young baboon attracts only a single bachelor, who approaches the young animal, with whom he may then assume friendly relations.

The range of the sexual activities of the young males is very wide. By the time they achieve some measure of independence—that is when their movements are well co-ordinated—they are adapted to a social system ruled by dominance. They present in situations which provoke fear. They employ sexual approach in obtaining access to each other and to entice a fellow for play. They masturbate and they mount each other. They mount and are mounted by adult males and by adult females, their heterosexual activities not provoking aggressive responses from the overlords. They engage in manual, oral and olfactory ano-genital examination with animals of their own age and with adults of both sexes. They frequently end a sexual act by biting the animal with whom they have been in contact. This end to sexual activity, which is not usually seen in the behaviour of adults, often appears to be playful, the young animal running away from his partner as soon as he has delivered the bite. Changes take place in the appearance of the immature males as they reach sexual maturity. Their greenish-brown coats change to grey, the hair of the back and shoulders grows into the mantle of the adult male, and they then join the band of bachelors.

In an earlier chapter it was mentioned that not many of the young animals bred on the Hill have survived more than a few months. The only exceptions have

been the female born in October of 1928, and the young male that was killed during an attack on its mother after she had been removed from the Hill. Thus there have been few opportunities in the London Colony for studying the early development of social behaviour in baboons.

The only animal in the social group whose behaviour at first is obviously modified by the birth of a baboon is its mother, since the event does not usually attract the notice of the other members of the colony. As a rule the newborn animal does not leave its mother's arms until about a fortnight has passed, and sometimes as many as six weeks may elapse before it sets foot to the ground. Individual differences may be observed in the amount of care a mother bestows on her offspring, but all closely watch the first movements of their infants. At the first sign of danger or fighting, the mother gathers up her baby, who in the early stages of its growth clings to the hair on her belly. As its movements become better co-ordinated it may ride like a jockey on her back. The mother baboon rarely plays with her offspring, and in few cases has the father ever been seen to pay it any attention. Once a male was observed tormenting his child, and on another occasion a male baboon was seen to gather up his offspring, embrace it closely and walk several paces with it. At the end of this performance the young animal ran eagerly to its mother. The usual indifference of the father baboon contrasts with the behaviour of the male chimpanzee which, according to Bingham,[39] plays more with his infant than does the mother, though he never takes care of the young animal. Von Allesch [23] reports that the female chimpanzee teaches her offspring to walk. No such behaviour has been observed amongst the baboons in the London colony, although when a baby goes too far afield, the mother is usually observed to grasp the nearest part of its body and pull it back.

In the early stages of the baby's growth the mother baboon usually snatches her infant up when the harem

PLATE XX

Photograph by J. L. Saunders

A YOUNG FEMALE BABOON AND THE BACHELOR WHO HAD ATTACHED HIMSELF TO

moves, but when the baby is about four months old and its movements are fairly well co-ordinated, it may either follow by itself, or jump unaided on to her back or to the hair on her belly, and so be carried. When it is about six months old, the young animal spends a great part of the day away from the immediate neighbourhood of its family, moving amongst the other animals of the colony. The reactions of the adult males and adult females to the young animal are very characteristic. As it passes them they may smack their lips and touch it with a hand. On many occasions adult females belonging to different harems have been observed to pick up a young animal belonging to another female, to embrace it, to groom it, and then to play with it. The form of their play is very distinctive, and often consists of a dance that is built up of incompletely formed somersaults. The bachelors show an equal amount of interest in young animals, although none has ever been seen playing with one. They confine their activities mainly to embraces and to genital examinations and grooming. The immature males are also greatly interested in a young baboon after it has attained a certain degree of independence. They play with it, sometimes roughly, and may be seen examining its genitalia and presenting to it. By the time it is about nine months old, the young baboon grooms those animals with whom it plays, and presents sexually in a variety of situations, some of which definitely contain an element of fear.* The sexual development of the young baboon is considered in detail in the next chapter.

The early social adjustments of the young female that was born on the Hill in 1928 present many points of interest. Until the death of her mother, her most constant relationship was with the bachelor attached to her family party, who, by the time she was nine months' old, was clearly treating her as a sexual

* A young female baboon, four months old, caught in South Africa, presented in many different situations.

object. On one occasion when she was ten months old, she was being sexually maltreated by him, and neither her mother nor her father, who were both in the vicinity, paid any attention to her struggles. After the death of her mother, and the consequent disruption of the harem, the young female was most commonly seen with another bachelor, who later became her only companion. By the time she was sixteen months old she rarely left his side, and when due allowance was made for her sexual immaturity, her behaviour seemed to differ in no significant manner from that of an adult female.

When the behaviour of a colony of captive baboons is observed over a long period, it becomes obvious that much variation occurs in its activity from day to day. Adult baboons spend the greater part of the time sitting quietly alone, in pairs, or in family parties. Every now and then they take up a new position in the enclosure, or move in and out of their sleeping dens. A baboon sitting alone may often be seen yawning. It is difficult to decide whether such a gesture always represents a dominant display, or whether it is sometimes yawning, in the human sense, from fatigue or boredom. The animals are more inactive in bad weather than on warm sunny days. As the sun appears from behind the clouds, they herald its advent with a chorus of grunts, and the warmth often stimulates a sudden display of sexual and grooming activity. Feeding times, when they run in a body to the heap of food that is poured into their enclosure, are among the few occasions when all the animals on the Hill exhibit the same response. Occasionally two or more adult baboons may be seen pursuing each other quietly round the rocks on the Hill. This form of behaviour is altogether different from the chasings that take place during fights, and its significance is not clear. It may be related to the running activities that were observed in South Africa * and which were interpreted as a form of play. There do not appear

* See Chapter XII.

to be any special territorial rights within the confines of the Hill, although on the approach of a stronger animal, a less dominant animal may be seen to vacate the place in which it has just been sitting. A dominant party of animals, such as a family, may, when on the move, attract both young animals and bachelors in its train.

Baboons usually behave in a hostile manner to their sick companions. An ailing animal often draws the attention of its healthy fellows, who gather, and threaten it, and who, by their persistently aggressive attitude, may goad it until it rushes at them. One day an immature male baboon had a fit, falling some six feet. As he lay, the limbs on one side of his body were twitching in an epileptiform manner. He attracted the momentary attention of one bachelor who soon left him, and then lay unconscious for some five minutes, finally staggering off alone.

Many characteristic vocal sounds are associated with specific social activities of baboons. The rhythmical lip, tongue and jaw movements that usually accompany friendly advances between two animals, and that continue throughout the process of grooming, make a low chattering sound which can be simulated by repeatedly pressing the tip of the tongue against the upper incisors. In more direct sexual activity this sound may give way to a rhythmical series of deep grunts, similar to those with which the animals greet the sun. These grunts are commonly made in all states of well-being. One grunting baboon seems to stimulate several others, so that the sexual activity of two bachelors may be accompanied not only by their own cries, but also by those of a number of their fellows.* Another characteristic cry of the baboon is

* The cries of one monkey often stimulate the same cries from its fellows. This may be observed among caged animals when excitement, initiated by the call of an animal of one species, spreads through all the cages of a monkey house, the cry being taken up by New World monkeys, Old World monkeys and even apes.

the high-pitched screech of a young animal or a female, made either in a situation of obvious danger, or in situations which to the human observer do not appear to contain any cause for fear. This cry usually attracts neighbouring dominant baboons. Sometimes adult males make a similar cry, but it is not so high-pitched and accompanies states of rage occasioned either by the attack of a more dominant animal, or by its own impotent attempts to attack a fellow. By attracting other animals it may begin a new fight. This cry is altogether different from the far-carrying, deep-throated barks heard in the wild when the members of a troop of baboons are scattered, or when a possible enemy, for instance a man, is observed approaching. This cry, which in the wild probably effects the reunion of a scattered troop, is only rarely made in captivity. I once heard a female barking this deep call after the death and removal of her baby. It is always heard when bodies are removed from the Hill, and is then raised by many animals. For several weeks after the females were removed from the Hill to a new cage some two hundred yards away, they continued to call in this way and to be answered by the males whom they had left behind.

CHAPTER XVII

THE DEVELOPMENT OF SOCIAL AND SEXUAL RESPONSES

THE development of human sexual behaviour is a subject that is hedged about with much superstition and crowded with prejudice. Hence it is not surprising to find that opinions differ concerning the parts played by heredity and environment in the development of human sexual responses. The problem is not one that lends itself readily to a scientific approach. Many projects for observing children in an environment unaffected by the behaviour of adults have been mooted, but abandoned because of the obvious difficulties. The results of the compromises that have been tried are disappointing, and they indicate clearly that direct observation of the growth of human sexual responses is impossible at the present time. Introspective analysis is also a somewhat disappointing approach to these problems, since the resulting testimony usually suffers from an added defect in this field, because it is affected by sexual restraints and inhibitions. The more the practical difficulties are considered, the more obvious does it become that at present there is no way of discovering exactly how much of an observed human sexual response is spontaneous and innate, and how much has been conditioned by a familial and social environment.

The study of the developmental stages of sexual activity in animals is a far simpler task. Its only subject matter are the data yielded by observation, data that can be statistically considered, and controlled through experiment. Thus Stone[339] found that young albino rats do not become sexually mature

until about forty-eight days old. He concluded that none of their activities before that age have any real sexual significance—in the absence of definition a somewhat arbitrary decision.[338] By isolating female rats from the time they were weaned until they reached puberty, He was also able to show that "no environmental influences or factors beyond those necessary to insure normal somatic development are required to bring about sexual maturity as manifested by ability to perform the copulatory act during the receptive phase of œstrus."[345] His experiment showed that an isolated female came into œstrus at the same time as she would have done if she had lived a social life, and that her mating responses were immediate when released by a situation that included an aggressive and potent male. In this way he was able to prove—so far as it is possible to do so—that the copulatory response in the rat is an unconditioned response, and that a rat gains nothing in its sexual development from a social environment. In another experiment he was also able to show that sexual development may be delayed by deficient diets.[342] Stone's experiments on rats represent the furthest point so far reached in the experimental analysis of sexual development in any animal.

Louttit's[237] analysis of the development of sexual behaviour in the guinea-pig yielded strikingly similar results. The guinea-pig becomes sexually mature at about the same age as the rat but, unlike the rat, the various elements that form the complete adult pattern of sexual behaviour appear serially. The first group of sexual activities appears in the male guinea-pig when it is between thirteen and seventeen days old. It then starts nosing and pursuing females—a form of behaviour that Louttit considers may not be exclusively sexual, since it is exhibited in all situations in which there are two or more animals. Between the twenty-fourth and thirtieth days the male begins to exhibit a new set of reactions. He circles chattering round the female, and bites and nibbles her skin.

Seven days later the final elements of the complete copulatory pattern appear. The male runs close to the female, whom he mounts, although actual mating depends upon her receptivity. Louttit's experiments also show that isolation does not retard the exhibition of overt sexual adjustments. Like the rat, the guinea-pig does not need a social environment in which to develop its sexual responses.

Any decision that characteristic social activities appearing before puberty have sexual significance is necessarily somewhat arbitrary. Both the guinea-pig and the rat exhibit the actual mating response for the first time at puberty, but neither then nor in adult life does it ever appear as an isolated act. It is always preceded by certain activities to which some investigators apply the term "courtship". Louttit holds that the nosing and circling activities of the prepubertal guinea-pig are part of its sexual responses. Stone, however, considers that there is no more than social significance in the behaviour of the immature male rat when it fearlessly approaches and noses an adult female. He also states that genital examinations, which may take place when an immature rat explores its own or a fellow's body, are simply part of its investigatory reflexes, and that they are not associated with its subsequent copulatory behaviour. The differences between the descriptions of these two observers are probably due to the lack of any fixed definition of the term "sexual response", and as such they are relatively unimportant. What is important is their agreement that the final stage in the development of sexual behaviour is the appearance at puberty of the mounting response accompanied by characteristic movements. In both the rat and guinea-pig this series of motor activities appears suddenly for the first time at puberty.

As might be expected, the development of sexual behaviour in monkeys and apes follows an entirely different course. The complexity of the sub-human primate as a sensori-motor organism is far greater

than that of the rat or guinea-pig. The monkey or ape responds more quickly to new situations. Its investigatory reflexes are more numerous and much more highly developed. The movements of its eyes and hands are linked together, as they are in man, and vision plays a far greater part in directing the activities of sub-human primates than in directing those of the lower mammal. Moreover, instead of the month that in the rat or guinea-pig separates weaning from sexual maturity, the monkey has about five years—the ape about nine—of prepubertal social life during which its activities are not directed by internal physiological "drives", but by the multitude of exteroceptive stimuli presented by the social activities of its fellows. It is thus not surprising to find that the young ape or monkey reproduces all the activities of its elders, and that, so far as is physically possible, every sexual response of the sub-human primate is exhibited before puberty. At puberty these responses are given force, apparently by the sexual hormones, and their previously playful character is replaced by the seemingly purposive quality of most of the responses of mature animals.

The first external phenomenon of which a sub-human primate has any sensory experience is hair. As a baby monkey or ape is born it is pulled by its mother to her breast, and its fingers immediately clutch and hold her fur. The type of behaviour that would be designated "maternal care" is notably absent at first. Unaided, the young animal finds the nipple by "trial and error." For about the first month of its life it lives entirely upon milk, and is carried by its mother wherever she goes. When the mother is sitting, the young animal is generally held close to her body, with its feet clutching at the hair of her belly and its hands buried in the fur of her chest. When she moves the baby hangs on in the same way, slung, as it were, beneath her. Usually it holds on by its own unaided efforts, but sometimes the mother clasps it with one "arm", while she hops along on three

"legs". When she is sitting she may embrace her baby with both arms. The baby manifests a strong interest in fur. It crawls over the mother's fur; within a week it may scratch its own body. I once observed a monkey, a week old, vaguely exploring with its hands the fur of its father, who was sitting close to its mother. Sometimes the mother monkey behaves as though she were irritated by having her fur clutched. A pig-tailed macaque in the London Gardens persisted in pulling away the hands and feet of her infant wherever they clasped.

As soon as it is born the baby is immediately examined, licked, and picked over, as though the young monkey were "merely an object to be washed", as Tinklepaugh and Hartman have written.[359] From the beginning it is continuously examined by its mother. Its fur is explored, its eyes, nose, mouth, ears, and ano-genital region investigated, by her fingers, tongue and lips.

The young monkey whose development was followed by Lashley and Watson sat on the ground, clasped in its mother's arms, on the day it was born, and walked alone when twelve days old. The youngest monkey that I have seen crawling independently was thirteen days old. During the preceding days this animal, a baboon, had shown an interest in the ground, which it touched and rubbed with its fingers. From the time this young animal showed itself capable of independent movement, its mother constantly pulled it from her to the ground, and as it grew older her behaviour definitely suggested that she was avoiding contact with it. When she rose to move away, the young one would rush at her and clasp the hair of her belly, but often she would pull its tail and throw it from her. Such lack of maternal care is uncommon. Some baboons remain in their mother's arms for as long as six weeks before attempting to crawl.

Lashley and Watson [230] first saw signs of sexual activity in the Rhesus monkey they were observing when

it was about two months old. While its mother was grooming it she picked over its sex organs, and the young animal then showed an erection. The young baboon mentioned in a preceding paragraph was observed making rhythmical "pelvic" movements, when it was thirteen days old, the same day it was first seen walking. Such movements, as the following description indicates, may represent the earliest motor expressions of sexual mechanisms.

At this point mention may be made of two characteristic forms of behaviour exhibited by monkeys. The first is the series of rhythmical body and hind leg movements that help to make up the mating response of a monkey covering a fellow. They are exhibited by adult males and females alike, as well as by immature animals of both sexes. The second is the series of movements employed by a monkey violently shaking a perch upon which it is standing. This display is often exhibited by healthy and dominant males, and is common to many Old World monkeys. In the Monkey House in the London Zoological Gardens adult male monkeys, in an apparent burst of vitality, will sometimes jump vigorously on to the central perch passing through their cages and, grasping it with their hands close to their feet, shake violently, by means of a series of rapid rhythmical movements. The immediate interpretation suggesting itself to the observer is that this is a dominant display of power.* From this point of view it seems to be related to the copulatory movements of the monkey, which in a sense also manifest dominant power. Moreover, the two series of movements in some ways resemble each other overtly and, as the following description indicates, they also appear to be related ontogenetically.

* It is perhaps interesting to consider that such behaviour might be the basis of the many accounts, appearing in the literature, of monkeys hurling branches and fruit from trees. Powerful monkeys violently shaking the branches of a tree will undoubtedly dislodge loose fruits and dead branches.

PLATE XXI

Photograph by J E Saunders

A NURSING FEMALE BABOON AND HER OVERLORD

(See p 260)

A young pig-tailed monkey was born in the London Gardens on the 5th of July, 1928. As its vague movements became co-ordinated, it began to explore and move over its mother's fur—thus superimposing a social relationship of grooming upon their physiological relationship. Its mother's response to this increase in the range of its activities has already been noted in a preceding paragraph. She often reacted by pulling the young animal's hands and feet from wherever they clutched. The young monkey did not leave its mother's arms until it was three and a half weeks old, when it began to crawl along the floor and perches of its cage. As it became stronger, and its movements more certain, the range of its independent activities increased, and it began to extend its social interest to monkeys in neighbouring cages. Rhythmical shaking movements which it made when hanging on the wire of its cage and when standing on the perches, were the earliest distinct patterns of behaviour that it exhibited. These movements usually appeared sporadically during the course of ill-defined play activity, and from the beginning showed a striking resemblance to the exhibitions of vitality and dominance of more mature animals. When it was about six months old, it was seen on its perch varying such movements with similar movements accompanied by erection, which were unmistakably of a copulatory nature. The overt difference between the two kinds of movement was very slight, and over a long period the two alternated with each other. Although the "cross-sectional" nature of my observations do not allow of firm conclusions, they clearly suggest that the copulatory movements of this young monkey and the rhythmical movements accompanying the display of its vitality developed from a common foundation.

In the course of its ill-defined play activities the young animal frequently explored and picked over its mother's fur. Its sexual interest was first manifested by the attention it paid to the ano-genital region not

only of its mother, but also of its immediate neighbours, from whom it was separated by wire partitions. During its explorations of its mother's body, and often in the midst of play-fighting activities, it would suddenly stop and peer at her pudendal region. As it climbed over her body, it sometimes held on to her hindquarters, its feet clasped round her thighs and its hands clutching the fur on either side of her tail, remaining in that position for a moment or two before proceeding in its climb. When it was about six months old, it mounted its mother in response to her repeated presentation, and about a month later this activity was first seen to be accompanied by erection and by pelvic thrusts. About this time it was often observed presenting both to its mother and to neighbouring animals. Sometimes, when it mounted her, its mother pulled it off; at other times she seemed to incite it to cover her. At this stage the young animal still took the breast, was still occasionally carried in the ventral position, and always slept in its mother's arms. Their mutual relationship was therefore compounded of at least three elements; the maternal one, which involved nursing; the social one, which consisted in mutual picking, play activities and the protection she afforded it; and the sexual one, in which the young animal was, in a sense, its mother's mate. Its age of eight months corresponded, from the point of view of tooth eruption, to that of a child of about two years.

It cannot, of course, be supposed that the behaviour of this young animal was typical of the behaviour of all monkeys at the age of eight months. It was behaviour from which almost all inhibitory social forces had been removed. It is conceivable that it would not have been exhibited had the young animal's powerful father shared the same cage. The young monkey's socio-sexual activities often drew his displeasure in the form of violent lunges at the intervening wire partition. The mother continued to be

interested in her former mate, to whom she often presented. The inhibitory effect that a wider social environment may have upon the activities of a developing monkey is indicated by Lashley and Watson. These observers state that their young monkey showed extreme fear when introduced with his mother, at the age of four months, into a cage containing two males, one of whom was his father. The degree of relative independence that he had displayed when confined alone with his mother was now greatly reduced, and he seemed "in constant fear of his life, rarely even attempting to get away from his mother."

When the pig-tailed monkey was a year old, it was temporarily separated from its mother for three days. On the first day it seemed very dejected, whimpering and wandering in a frightened way to and fro in its cage. On the next day, it seemed accustomed to its solitude and was seen making rhythmical mating movements on the bar of its cage. Two days later, when its mother was reintroduced, it made no immediate attempt to approach her. It remained with her until it was sixteen months old, when they were finally separated, and it was removed to a cage containing several other young monkeys. Until the time of separation its behaviour did not assume any new elements. It continued to mount its mother and to show interest in the neighbouring animals, to whom it presented.

The mother pig-tailed monkey gave birth to another baby, a female, twenty-three months after the birth of the young animal whose development has just been described. As before, the father was moved to another cage on the day of the birth. The sexual development of the young female followed a course similar to that of its brother. When about seven months old it responded to its mother's presentation by mounting. When it climbed too high on her rump, the older animal pulled it down. This behaviour often ended in undefined play activities, in which the young animal

jumped on to its mother's back and head, and fought playfully. Occasionally the mother seemed to be irritated by its behaviour and repulsed its advances.

The sexual interest shown by baboons in young animals born on Monkey Hill has been referred to in preceding chapters.* Further notes on the socio-sexual development of the young female born in October, 1928, may be quoted here.

Mention has already been made of the growing independence of this young animal from the time she was about six months old, and of her social adjustments with the immature males, bachelors, and females of different harems. Fear responses were noticed before she was six months old. In this her development was comparable with that of the young macaque observed by Lashley and Watson. Once she was frightened away from a bachelor with whom she had been playing, by a sudden attack launched upon him by her father. On another occasion she ran screaming from two bachelors who were fighting over her. When she was seven months old, she was observed lying on her back, being pressed and mauled sexually by the bachelor attached to her family party. Another bachelor, attracted by her squeals, came up and threatened her tormentor, who repelled him while still retaining his hold on the baby. He then made off with her, holding her closely in a "maternal" embrace. Two days later she was observed being covered sexually by an immature male who was inclined to be rough in his play. She had approached this animal first, running up to him and prodding him. After covering her sexually, the young male embraced her and began to groom her. Their play continued for some time within two feet of her mother and father. Suddenly the little male pushed the young female on to her back and made copulatory movements, with erection, over her body. This is the only occasion on which I have observed baboons of any age attempting

* See Chapter XV, p. 245, and Chapter XVI, pp. 261, 262.

to mate in this manner. About this time she was often seen presenting, and when she was eight months old she was observed engaging in mutual genital examination with adult males, who in their sexual reactions towards her treated her as an adult female. One day an adult female, belonging to a different harem, was observed covering the little female and making copulatory movements over her. From the time she was sixteen months old until, eight months later, she was removed from the Hill, she was always with the same bachelor. Their mutual behaviour was almost identical with that of a pair of adult animals, except that complete intercourse was impossible because of her size. Her further behaviour with this male, after her removal from the Hill and her introduction to cage life in new social surroundings, has already been described.

When the development of this baboon is compared with that of the young males of the baboon colonies, it is clear that all the manifestations of adult sexual life have developed by about the time that the milk dentition is completed, that is to say, when the baboon is about nine months old. By that time the animals are fully adapted sexually to a social life that is based upon a system of dominance.

Sexual development is relatively slower in the anthropoid ape than it is in the monkey. Early sexual activities are shown, but as a rule the accomplished sex play of the immature monkey is not exhibited, and the final adjustments for mating may not appear until after the sexual experiences of maturity.

The early stages of growth in the ape correspond closely to the similar stages in the monkey. Like the monkey, the chimpanzee develops its sexual responses in a social group, but its prepubertal life is much more prolonged, lasting from eight to ten years. Young apes, although they engage in mutual contacts from a very early age, do not present to nearly the same extent as do immature monkeys. Presentation becomes a

common response only towards puberty. In their social contacts the young animals often examine each other's bodies and display great interest in the genitalia. Such investigations become frequent in the later stages of childhood. In the earlier stages bodily contacts mainly occur in the rolling and fighting of their play activities, and in situations of fear, when the young animals embrace one another. The erectile organs of both male and female apes show activity very early in life, and are stimulated in a variety of circumstances. Thus the animals show erection when they are petted by human beings, when they are tumbling about together, and when they are engaged in mutual bodily examinations.

When two young apes are introduced to each other, or when a new animal is added to a pre-existing social group, it is usual for a certain amount of play-fighting to take place. This social response is not accompanied by signs of great excitement, and it may continue for a considerable time. In the Zoological Gardens it is more commonly exhibited by the more mature newcomers—those of about the age when their first permanent molars erupt. Younger animals—those at the age when the milk teeth have just erupted—are more subdued, and as a rule immediately run to the animal to whom they are introduced, attempting to embrace it. Individual differences are also observed among the older immature animals. When placed in a cage with a group of socially adjusted apes, some chimpanzees do not resist the pummellings they receive at the hands of the older inhabitants, and as soon as hostilities cease, keep quietly to themselves. Others seem to enter more readily into the spirit of the play, and by resisting the attacks of the already socially adjusted group, prolong the combat. A young spirited male chimpanzee was introduced into a cage in which were living two females who had already been together for two years and were thus completely adapted to each other. One of these females was nearing puberty and

her permanent teeth were erupting. She was a much bigger animal than the other female, who at the time had only one tooth of her permanent dentition. The male had his milk dentition, and was the smallest of the three. All three animals immediately responded by fighting. Both the females made for the newcomer, who resisted and tried to bite and "knock them about". The combined weights of the two females frequently forced him to the ground in a close scrimmage, in which his body was pounded and bitten. But he usually managed to escape. Both females, when they had an opportunity during a lull in the combat, examined his genital region. The older female was the more persistent in this behaviour. The male did not reciprocate these attentions. The play-fighting activities and bodily examinations continued intermittently throughout the first afternoon the animals were together. By the next day they were fairly well adapted to each other and no further attacks took place. The young male maintained a great deal of independence, and in no way disturbed the pre-existing relationship between the two females. This playful form of fighting usually continues long after the social relationships of the new animals are mutually adjusted.

Bingham [40] has published the results of an extensive study of the social and sexual development of four young chimpanzees. These were obtained in pairs—Wendy and Pan, Dwina and Billy—the members of which had been together for some time before they were bought. In spite, however, of their pre-existing social adjustments, certain rearrangements took place when the four animals were introduced to one another. For a relatively long time, Dwina and Pan remained on somewhat playfully aggressive terms, and while they were engaged in their romping activities, Billy and Wendy began to play sexually, their activities culminating in ventral copulation. Bingham draws attention to the surprising sexual "co-operation" of these two immature animals, and compares their behaviour

with the unsuccessful mating activities of two almost mature chimpanzees he had observed in Cuba. He also comments upon the lack of excitement shown by young animals engaged in sexual activities. Rivalry developed later between Pan and Billy, and Pan was seen mounting Wendy, but neither animal spent much time in sexual play with the oldest member of the group, Dwina. In spite of her sexual adjustment to Billy, Wendy's "abiding social interest" remained in Pan. "With him she sleeps and with him she stays when the playful activities of the group wane. . . . To him she runs for mutual embracing and clinging in the face of danger or threatened separation." Like Wendy, Dwina also retained closest social interest in her own partner, Billy.

Bingham's chimpanzees showed considerable variety in their sexual expressions. Hanging on to a grill, Wendy presented to Billy—behaviour which Bingham considers exhibitionistic. It resulted in Billy showing an interest in her protruding genitalia, which he picked with his fingers and took in his lips. Finally he covered her, and during the prolonged copulatory play that followed, Billy several times took "some part of Wendy's anatomy" in his lips, and persistently mouthed her external genitalia. Bingham had previously observed similar behaviour in the activities of an eighteen months old chimpanzee which was playfully exploring its mother's body, and he thus interprets it as a reaction belonging to the earlier stages of the chimpanzee's life, and one that is related to the suckling response.

Observations of anthropoid behaviour comparable with those just referred to have been made in the London Zoological Gardens. A young male orang, and a young female chimpanzee, neither of whom yet had any permanent teeth, arrived in the Gardens in October of 1928 and were confined together in a small cage. They were perfectly healthy animals, and neither showed any fear of the other. From the start, and until they

were separated four days later, their behaviour was predominantly sexual, the orang being the more aggressive partner. As he hung with his arms from the top bars of the cage, with one foot clasped round the perch on which the chimpanzee sat, he repeatedly made copulatory movements, with erection, towards the young female, thus achieving mutual genital contact. The placid character of the performance contrasted greatly with the excitement that usually accompanies the sexual activities of adult animals. The young apes varied this behaviour with mutual genital examinations—the orang again being the more aggressive of the two; and for long periods on end, he held the chimpanzee's external genitalia between his lips. This activity showed many resemblances to suckling behaviour.

An interesting observation recorded by Bingham is that sexual activities can be induced by separating and re-uniting a pair of young chimpanzees. A similar observation had been made by Köhler, who found that great excitement is stimulated when a chimpanzee that has been isolated for some weeks returns to his group. "They put their arms round him, even beat him a little for pleasure, and often the whole bunch run along behind their returned companion, as is the habit of chimpanzees, in order to examine minutely his rump and sexual parts." [217]

Pronounced temperamental differences are shown by chimpanzees in their socio-sexual relations. For example, Bingham's chimpanzee, Billy, indulged in prolonged sexual play with Wendy. Pan, on the other hand, was very quick and direct in his sexual contacts. Both strongly reacted sexually to Wendy, but neither made sexual approaches to Dwina. The amount of their sexual activities also varied considerably from time to time. In some months they were completely in abeyance, while at other times they were greatly exaggerated.

The prepubertal sexual behaviour of chimpanzees is not limited to heterosexual relations. Homosexual

activities are also displayed. Dwina was the biggest and most dominant of Bingham's apes and, at first, her physical relations with the other animals—apart from those accidentally brought about in play—were limited almost entirely to embraces in which she held them in a protective manner. Later her attitude became more obviously masculine. On one occasion she took Wendy's external genitalia in her lips—although in contrast to the behaviour of the others, she herself was indifferent when her genitalia were touched. As if she were a male, she frequently covered Wendy, and occasionally she also made ventro-ventral genital contact with her. Bingham records an earlier observation which he made of more mature female chimpanzees behaving homosexually, and draws attention to the fact that again it was the bigger female who played the part of the covering male. He also describes a particular homosexual response in which the females made mutual genital contact by standing on all fours with their faces in opposite directions. Similar behaviour between adult female bonnet monkeys has been observed in the London Zoological Gardens. Fewer homosexual activities were observed between the two males, Billy and Pan, of Bingham's group, than between the two females, Wendy and Dwina.

Considering the ill-defined and varied nature of their sexual responses, chimpanzees masturbate very little. The onanistic practices of the female are much more varied than those of the male. She uses fruit, bottles and twigs as sexual objects, and she often also brings her genitalia into significant contact with the ground, with the walls and with the wires of her cage. A cat was used as a sexual object by a female chimpanzee investigated by Bingham, while the immature female gorilla, Congo, investigated by Yerkes, showed prolonged sexual interest in a dog with whom she had assumed a dominant rôle. Immature chimpanzees of both sexes often make sexual advances to human beings.

On the basis of his studies, Bingham has tentatively

suggested a list of activities which in the chimpanzee make their first appearance as non-sexual acts and which later become re-synthesized in adjustments of a copulatory nature. Both sexes develop some facility in all these responses, although one sex may specialize more in some than in others. His list of copulatory antecedents is as follows:

"(1) Clinging, cuddling, and embracing.
(2) Explorations and manipulations: manual and oral contacts as in boxing, pulling, pushing, and picking; nuzzling, sucking, licking, and biting.
(3) Flight, retreat, and evasion, often leading to (1).
(4) Play threats, erect advances, and fighting leading to (1) or (2).
(5) Tantrums and borderland behavior between fleeing and fighting which encourage responses from a companion similar to (1) or (2).
(6) Ornamentation,* coquettish play, and secretive play serving as invitations to a companion which lead to (1) or (2).
(7) Erection reflexes in male or female which appear early and under various kinds of non-sexual excitement.
(8) Stimulation of genitalia by contacts involving individual adjustments."

Bingham points out that many of the elements of mating behaviour appear

"no later than the early hours of post-natal life . . . Such phenomena as clinging, embracing, mouthing, manipulation,

* Bingham draws attention to an occasion when an almost mature female chimpanzee carried a mango on various parts of her body, later using it as a sexual object in masturbation. Mainly on the basis of this observation, he has suggested that ornamentation is a phase of play which may have sexual significance. The ill-defined character of the "ornamental play" of sub-human primates makes it difficult to accept this view. There can be little real difference in behaviour between an adult female chimpanzee carrying a mango on her head and an immature male baboon that runs about with a basket on his. To suggest that there is a significant difference is to take a very anthropomorphic view of such activities; and to suggest that the act of the young baboon is sexual is to make an assumption which is unsupported by any evidence.

pelvic pushing, and erections, all appear under diverse conditions in advance of recognizable copulatory behavior. Their assemblage in novel sexual adjustments seems, after review of their genesis, to be largely an old story with the details more or less rearranged."

According to the same author, the facts suggest both a gradual and sudden emergence of sexual reactions.

"There may be a quick reorganization, an unexpected adjustment, but when the antecedent behavior is reviewed after the initial adjustment has been observed, one may trace, if the background be adequate, a gradual preparation for this consummation. The novelty observed in the initial copulatory adjustment may be nothing more than a new combination of old response factors. The continuity seems to lie in the familiar units of response that have often been expressed in previous adjustments of a different nature."

In the chimpanzee the final adjustments and rearrangements of these elements usually occur after puberty. The ventro-ventral sexual contact so commonly observed in the play of the immature animals becomes replaced by the dorso-ventral position. This change coincides with a growing attitude of dominance in the male ape as he obtains his full complement of permanent teeth, and as his strength and vitality increase. An animal of this age in the London Zoological Gardens walks defiantly about his cage, sometimes on all fours, sometimes upright. His hair bristles and his whole demeanour is one of vigour. He drums on the walls of his cage and, violently shaking his body, clatters a movable platform, then jumps aggressively to the bars to threaten the human beings who have gathered to watch his behaviour. He fills his mouth with water and sprays the curious observers. His attitude is one of complete confidence.

Yet the dominant and almost mature male chimpanzee is unable, so far as observations have shown, to perform the mating act adequately. Bingham conducted an initial mating experiment at Madame

PLATE XXII

Photograph by J E Saunders

THE BABY BABOON BEGINNING TO WALK

Its mother's hand is raised, ready to lift it from the ground (See p 260)

Abreu's colony in Cuba. A dominant male, nine years of age, was led into a cage that contained a slightly younger female. Although she appeared to be receptive and anxious for sexual advances, the male responded as ineffectively as an immature animal might have have done. Similar initial mating "experiments" have been carried out in the London Zoological Gardens. The male chimpanzee whose behaviour is described in the preceding paragraph arrived in the London Gardens on July 25th, 1926, and for over two years lived in the same cage with three younger animals. He was separated from them because of his dominating and aggressive behaviour. No record of his early social relations is available, but there is little reason to suppose that his development differed from that of other captive chimpanzees. After leaving the three younger animals, he was caged with a nearly mature female with whom he stayed for a few months and by whom he was completely dominated. No sexual activities were noticed while he remained with her. After her death he occupied the cage alone. About a year later a fully mature female chimpanzee, a recent arrival in the country, was placed in an adjoining cage, so that the two animals were able to inspect each other through the bars of a communicating grid. The male, who by this time was nearly mature,* was stimulated to very dominant behaviour. He strutted around his cage and beat violently on the communicating iron door below the grill. After five days' acquaintanceship of this kind, they were introduced to each other early one morning. At first both seemed rather frightened; but soon the male became aggressive, approaching the female in an upright position, with waving arms and swaying body. She immediately retreated. After this behaviour had continued for some time, the male seemed to lose interest and the female became the aggressor. She advanced and, to the surprise of the observers, beat her chest as a gorilla is reputed to do,

* His third molars had not yet appeared.

stamped her feet and beat a tattoo on the walls. For short periods the animals made bodily contacts, but neither showed any sign of mounting, although the male had transitory erections. At the time of this meeting the female's sexual skin was inactive. After an hour had passed the animals appeared to be avoiding each other. During the three months that they remained together, they were often seen play-fighting and making mutual bodily contacts in which fingers, toes and lips were used. Their social relations did not seem to develop beyond this level, although a keeper once reported having observed the male covering the female.

After this female's removal, the male was alone for seven months before a slightly younger, although sexually mature, female, who had lived mostly alone for five years in the London Gardens, was introduced to him. The male immediately dominated in the new situation, and the female appeared to be contentedly submissive. Neither showed much aggression. They have now been together for three months, and during this time their behaviour has been closely observed. The female has made sexual advances, but the male has paid no attention to her repeated presentations, and has never been observed covering her. Their mutual relations have not advanced beyond the stage of play-fighting and mutual bodily examinations, in which the female is more active. The male remains the dominating member of the pair, but his continued displays of vigour and vitality seem to have no connection with the female's presence in the cage.

These observations perhaps indicate the important part played by experience in the sexual activities of apes, and also the striking contrast between the sexual behaviour of the sub-human primate and the innate sexual responses of rats and guinea-pigs.

In discussing the results of his investigations, Bingham has suggested that the ventro-ventral mating contact of young chimpanzees is evoked during play

activities, particularly those of petting and teasing, whereas the dorso-ventral position—the position of the adult animal—is evoked as "a diverted response from a mixture of anger and fear". Reference has been made in an earlier chapter* to his view that the act of sexual presentation in situations which in themselves are inherently asexual begins developmentally, in the chimpanzee, as an inhibited flight from a situation that has induced fear or rage. This view was made the basis of a discussion in which it was suggested that fear and rage are emotions which are induced by a situation in which an animal is dominated. It was argued that the act of presentation may thus represent an act of submission before a dominant animal who, at the moment, is exercising its dominant character. The apparently complete replacement of the ventro-ventral by the dorso-ventral mating position at the time of puberty in the chimpanzee, may perhaps be explained according to this view. As the young animals grow, sexual dimorphism becomes increasingly obvious and, by the time of puberty, females are completely dominated by older males and by males of their own age in situations that have socio-sexual significance. The dorso-ventral position thus becomes the representation of sexual submission. Dwina, Bingham's eldest chimpanzee, played "little or no part" in the hetero-sexual activities of the group. This fact may also perhaps be explained according to the view outlined above. As the dominating animal, it was her part to cover her younger fellows. She was frequently seen covering the female Wendy, and was always dominant in her contact relations with Billy and Pan, although she rarely mounted them. The assumption of the inferior position would have conflicted with her status in the scale of dominance. She was never observed being covered by Pan or Billy. Bingham, in explaining her sexual aloofness from the group, suggests that the underlying cause may have been her "superior strength,

*See pp. 233, 239.

independence, and ability to dominate." It remains to be seen whether or not further observations on chimpanzees and other anthropoids will establish his claim that the two modes of mating response are temporally separated and significantly different from each other. Studies of the sexual development of the orang utan may perhaps shed some light on this problem. The mating position of the adult of this species is, so far as is known, ventro-ventral, and it is unlikely that this animal exhibits no behaviour to which the term "sexual prostitution" could be applied. On the view that sexual presentation is representative of an incipient reaction of flight from a situation in which an animal is dominated, it is obvious that the act of presentation of this animal would conflict with its copulatory adjustments.

Whatever may be its genesis, the act of sexual presentation is either a reaction to enteroceptive stimuli determined by the activity of the gonads, or a reaction that is stimulated by exteroceptive stimuli arising in a variety of social situations themselves inherently asexual. The majority of the more obvious presentations of the former group, together perhaps with all of the latter, are manifestations of situations in which the presenting animal is dominated. The response is exhibited by both sexes. In both, moreover, it stimulates mounting behaviour. It is interesting therefore to consider whether or not the mounting activities of males and those of females—discounting the question of reproductive function—are compounded of fundamentally different responses. As a corollary to this question it might be asked whether or not the terms homosexual behaviour and heterosexual behaviour have any basic significance with reference to the sexual activities of sub-human primates, apart from denoting the sexes of the animals engaged in sexual activity.

In discussing the latter question, it is unnecessary to consider the bodily examinations carried out by monkeys and apes. The form they take is the same

in both sexes and there is obviously no real difference, especially when the social activities of young animals are considered, between the behaviour of a male examining the ano-genital area of a fellow male and its behaviour in a similar investigation of a female. When these activities are discounted there remains for consideration such behaviour as might be termed homosexual. Amongst males such activities have a characteristic form. One assumes a feminine rôle and is mounted by the other. Amongst females, two distinct types of so-called homosexual contact may be recognized. The first is parallel to masculine homosexual activity, one female assuming the masculine rôle and mounting a fellow female. The second form has been described in a preceding paragraph, and is manifested by two females achieving mutual genital contact when standing on all fours, facing in opposite directions. The meaning of the latter response cannot be discussed, since nothing is known of its development, and since, so far as can be seen, it has only twice been recorded. It is perhaps significant that these two observations were made of female sub-human primates living in cages isolated from males, and that this response has never been observed among female baboons living in a colony. Whatever its meaning, it is a response which, compared with the first form of female homosexual contact, is rarely exhibited.

The muscular movements concerned in heterosexual behaviour and in the homosexual activities of both males and females are almost identical. In both, one animal assumes the dominant or masculine rôle, while the other takes the feminine or submissive position. The relevant muscular mechanisms remain practically unchanged throughout the animal's life history, but its responses vary in intensity from time to time. Except in adult life, when they become linked to the function of reproduction, the responses appear diffusely, in both sexes without any specific sexual stimulus and in almost any circumstances. Thus, when the overt

manifestations of sexual activity alone are considered, there does not appear to be any significant difference between the non-reproductive mounting behaviour of males and that of females.

If then, there be any real difference between homosexual behaviour and heterosexual behaviour amongst sub-human primates, it is in the underlying stimulus and not in the overt behaviour itself. In considering this question it is better to discount the sexual activities of adults, since physiological factors drive the mature animals of both sexes more in the direction of heterosexual activity, even though they still continue to engage in homosexual activities. One has to examine the sexual responses of immature monkeys and apes to discover whether or not either sex shows a preference for heterosexual or homosexual contact. My own opinion, based on prolonged observation, is that neither sex, especially among the younger immature animals, shows any preference for a particular form of sexual activity. The opposite view, however, is commonly held, certain observers, for example, maintaining that the young sub-human primate has a special regard for human beings of the opposite sex. Thus Bingham reports that his young male chimpanzee never made adverse demonstrations towards women, who were, however, often bitten by his two female chimpanzees. These in turn never attacked men. Moreover, his male chimpanzees made sexual advances to women visitors to his laboratory. Bingham also maintains that in its copulatory play, the young male chimpanzee, Billy, was more curious about the genitalia of his female companion, Wendy, than he was about those of his male companion, Pan. It is questionable whether the conditions under which these observations were made were sufficiently controlled to allow of the definite generalization that these young chimpanzees had stronger heterosexual than homosexual tendencies. Thus Billy's greater sexual interest in Wendy than in Pan may have been due, in part at any rate, to the

fact that he dominated Wendy and he, in turn, was dominated by Pan. It is possible, moreover, that uncontrolled social situations involving human beings as well as sub-human primates are too complicated to allow of any interpretations of the separate sub-human social relationships that exist within them. It would be comparatively simple so to control the human element in the experiment that its effect could be identified in the end-result.

Even if it be shown that young sub-human primates have a stronger heterosexual than homosexual tendency, the facts nevertheless suggest, if reproductive function is discounted, that no significant difference exists between the manifestations of these different tendencies. It might be suggested that, from the time a monkey's or an ape's movements become well co-ordinated, the animal lives in a social environment which provides stimuli to sexual responses. In a particular situation, the animal assumes the dominant or male sexual rôle, while a fellow assumes the reciprocal and submissive rôle of female. Such behaviour might be either homosexual or heterosexual. Mounting behaviour therefore depends fundamentally upon degrees of dominance, and at this level of analysis it seems purely accidental whether a particular response is homosexual or heterosexual in its manifestations. A constantly varying social environment provides stimuli to evoke the sexual responses in animals who themselves are from moment to moment varying in their mutual adjustments of dominance.

Upon this fundamental level of social relationships, dependent upon dominance, are superimposed two other levels, the one formed round play activities, the other dependent upon the physiological factors of reproductive maturity. It is conceivable that the level of playful sexual activity might simply be a manifestation of a rapidly varying interaction of dominant relationships, determined by excessive and growing vitality. The reproductive level of sexual activity

represents, however, something new in the socio-sexual life of the maturing sub-human primate. The physiological changes of puberty give meaning to sexual adjustment. They give them "drive" from a reproductive basis, and evoke responses, both heterosexual and homosexual, with a force altogether unknown in prepubertal life. But these responses are still directed within a social system based on dominance.

In describing our present knowledge of the socio-sexual development of apes and monkeys, this chapter has also revealed how scanty this knowledge is compared with the established data concerning similar developments in lower mammals. The rat and guinea-pig develop the effective elements in their mating adjustments suddenly and dramatically at puberty. They appear as the final elements in a gradually unfolding pattern of motor mechanisms. Apes and monkeys, as the facts have shown, seem to be entirely different. Almost every element in the series of motor mechanisms concerned with their mating behaviour appears early in prepubertal life, to become synthesized into the effective mating response long before physiological sexual maturity is reached. Such maturity provides only the final direction and force to these activities. Thus in many ways monkeys and apes run parallel to human beings in their sexual development.* Facts are not yet available to indicate definitely in what part the perfected sexual responses of the sub-human primate may be innate, and in what part conditioned. Those that are available suggest that social conditioning plays the bigger part. The investigation of the problem is complicated by the

* Freud states that sexuality during the early stages of human life is essentially auto-erotic and composed of numerous impulses, mostly independent of one another but all striving for pleasure. Final sexual development comes at puberty, when the acquisition of pleasure becomes linked to the function of reproduction, and the separate impulses of childhood are organized, under the primacy of a single genital erogenous zone, for the attainment of the sexual aim in a strange sexual object.[116A]

PLATE XXIII

Photograph by J. E. Saunders

THE BABY BABOON BEGINNING TO CLIMB

(See p. 260)

[*face p.* 290

monkey's sociality, by its great vitality, by the multitude of its investigatory activities, and by the rapid adaptation it shows to new situations. The problem could, however, be approached experimentally, by replacing the rats and guinea-pigs of Stone's experiments by monkeys born in captivity.

CHAPTER XVIII

ALTRUISM AND SOCIETY

MUTUAL help, according to teleological thought, is the underlying purpose of society. Sheep live in flocks because it is wiser for them to do so; a single animal would be defenceless against attack. Even predatory animals sometimes find it necessary to band together. Thus wolves are often reported to hunt alone in the summer, when food is plentiful, and to unite and pour into villages to snatch up defenceless babies in the depths of winter. Although all such superficial interpretation of social behaviour is biologically unsound, and although the statements out of which the concept of mutual co-operation primarily arises are mostly open to question, it is nevertheless necessary to examine the possibility of altruism existing in the actions of animals as social as the sub-human primates.

As the anecdotes related in the opening chapter of this book show, the behaviour of sub-human primates is commonly believed to indicate mutual aid. Thus, according to narrative, monkeys press leaves into the wounds of their fellows to stop the blood. In consideration of their dubious origin, tales of this kind may be disregarded. There are, however, other accounts of the assistance afforded each other by monkeys and apes that have received ample corroboration. Stevenson-Hamilton[337] relates how he once surprised a large troop of baboons in the bush. All except one scampered off, this animal taking refuge in a tree which was too far separated from neighbouring ones to allow it to leap to safety. Thus marooned, it immediately began calling, whereupon the whole troop came back, running about and barking on the fringe

of the bush, about fifty yards away. Although greatly excited they would not leave the shelter of the low trees to cross the open space that separated them from their isolated companion, who was finally captured. When this was done, Stevenson-Hamilton approached the rest of the troop. They began to retreat slowly, but it was not until a big male had been shot that the whole troop fled.*

Hunters who have once shot a monkey commonly relate that they were so appalled by the human behaviour of the wounded animal that they vowed never to shoot another. This sentiment is well expressed by Fitzsimons [107] who, with a friend, once shot a monkey that was nursing a baby. The monkey received the charge of shot in her back and came tumbling down from the tree, still cowering over her young one.

> "Hugging her baby tight to her breast, she regarded us with a world of sadness in her eyes, and with a gasp and shudder she died. We forgot for the moment that she was but a monkey, for her actions and expression were so human, that we felt we had committed a crime. Muttering an oath, my friend turned and walked rapidly off, vowing that this was the last time he would shoot a monkey. 'It isn't sport, it's downright murder,' he declared, and I fervently agreed with him."

Apart from indicating certain noble attributes of the human mind, these accounts provide evidence that subhuman primates in the wild give assistance to one another and that nursing monkeys continue to show maternal care when they are attacked. Such behaviour is also manifested in captivity. It is well known that a man tormenting or hurting one monkey of a cage may

* This was the only occasion on which Stevenson-Hamilton experienced resistance from wild baboons. On none of the baboon hunts in which I myself have participated could I recognize any behaviour that could be interpreted as showing mutual help on the part of the hunted animals. Thus, on many occasions, when separated younger animals were plaintively barking, the adult baboons did not return to assist them. At no time, moreover, did I observe any co-operative behaviour in the activities of the driven animals.

draw the threats of all the inmates, who run to the wire, stimulated apparently by the attitude and cries of their companion and the offensive demeanour of the man. Köhler [217] writes that great excitement prevails if a chimpanzee is attacked before the eyes of its group. "It will happen that, under the influence of the climate, one punishes a wrong-doer with a heavy blow. The moment one's hand falls on him, the whole group sets up a howl, as if with one voice." When dealing with the more mature apes, Köhler found that it was dangerous to punish a chimpanzee because of the tendency of the group to repel any assault made upon one of its members. The ape's first cry "in anger" calls together all its fellows, who rush to the attack, with "no notion of what it is all about. The only thing necessary to the uproar is that that scream shall be uttered in that characteristic manner that whips up all the others." Köhler also writes that great individual variation exists in the tendency of different apes to incite a herd to attack. Some animals fly into a rage over nothing; others are more placid. Moreover, as was indicated in an earlier chapter in this book, a monkey may give the "attacked" cry for no apparent reason. This cry brings upon the scene some of his fellows, who rush up aggressively and threaten or attack either the animal at whom he may be staring, or one another. Again, when one monkey of a group has to be removed from a cage, its fellows rush forward to threaten the interfering keeper. Sometimes, too, if a keeper, by throwing stones, tries to make a baboon on Monkey Hill move, its fellows rush forward aggressively and threaten him with grimaces and barks.

These facts clearly show that when one member of a group of monkeys or apes is attacked or threatened, its efforts at retaliation are supported by the aggressive responses of its fellows, aroused apparently by its cries, its attitude and the threatening demeanour of its attacker. There is also clear evidence that the support monkeys give one another in an attack is evoked, not by any intelligent apprehension of the nature of the

situation within which they release their aggressive activities, but as an immediate response to the stimulus of, for example, a particular cry emitted by the offended animal. Moreover, many of the occasions on which an ape or monkey comes to the assistance of a weaker fellow who is being bullied by another, appear simply to be exhibitions of dominance. Both the weaker animal and its tormentor may suffer from the sudden assault of the dominant animal. The response of a dominant animal to the "fear-threatening" gesture of a weaker fellow is also apparently as reflex in character as its reaction to the squeal of terror of a dominated animal, and neither situation seems to involve a feeling of sympathy in the sense this term is used in describing human behaviour. Nevertheless, although the "blind" nature of their mutual support seems to conflict with the concept of social altruism, it is a significant fact that such support is sometimes given.

The existence of mutually co-operative behaviour in moments of attack contrasts strongly with most social relations prevailing within the group. Monkeys as a rule either attack their sick and weak companions or ignore them completely. Powerful apes and monkeys will, in the midst of a dominant display, suddenly and without apparent provocation, attack their weaker fellows. In their behaviour at feeding times, monkeys and apes display the most conspicuous selfishness. With few exceptions, every monkey or ape living in captivity tries to obtain as much for itself and to take as much as it can from its fellows. Reference has already been made to the fact that the allocation of food within a group of monkeys depends upon the existing scale of dominance. The dominant animals as a rule obtain all of a limited food supply. It is a common experience that when food is passed into a cage of monkeys, the more dominant members come forward to accept it, pushing aside their weaker fellows who may have preceded them. When a number of bananas were thrown to a Monkey Hill family party consisting of a male, a female, and her

baby, which had been born about half an hour before, the male crammed his cheek pouches full of fruit, keeping at his feet what he failed to push into his mouth. The female made no attempt to secure any. If males behave selfishly to their females, females behave as selfishly to their young, snatching every piece of food that is offered, even from the very hands of the infant. When a small baboon is eating and a dominant fellow approaches, the young animal may stop and drop the food from its mouth in evident terror. Alverdes,[24] who states that it would be unwise to regard animal behaviour "from a sentimental point of view", nevertheless writes that such selfish feeding behaviour is an effect of life in captivity. This opinion obviously conflicts with his own precept, since there is no evidence available to support his view. However, it is unlikely that as much opportunity for the exhibition of selfish behaviour in relation to food would arise in a natural environment, since usually the abundance of fruits and leaves satisfies all.

The selfishness and cruelty engendered by a system of dominance stand in striking contrast to the support afforded one another by sub-human primates on occasions when they are attacked. Theoretically there are two groups of circumstances in which such support may be given. The first consists of those cases in which the support of a dominant individual is evoked either by a squeal of terror, or by a "fear-threatening" gesture unassociated with any event existing outside the group. It has already been pointed out that the giving of such support is in the nature of a reflex, and that the form it takes will depend upon the scale of dominant relationships within the group of animals concerned. As such it has, perhaps, no right to be called "mutual aid", in the sense in which this term is used in describing human behaviour, and the "rescue response" becomes yet another overt manifestation of a system of dominance, involving, as it does, a clash within the group. Thus, fundamentally, the "mutual support" afforded in situ-

ations of this kind is stimulated by the same factors that produce the effects of selfishness and cruelty. The second group of circumstances within which "mutual aid" is given, consists of those where one monkey or ape of a group is attacked or threatened either by an animal of the same species belonging to a different group, or by some animal of another species: for example, a human being. Fundamentally, the aid given in such a situation is also evoked in the manner of a reflex. The group responds immediately to the howl of rage or terror from the attacked member and to the aggressive attitude of the attacker. Although all the evidence is against a view that the response is ideational in character, and supports the view that it is identical with the first type of "rescue response", there is, nevertheless, some theoretical justification for regarding it in a separate category from the latter, since it does not involve a clash between the members of the group. From this point of view, the second type is a group response, and in spite of its "blind" character, which is discussed below, it may perhaps be regarded as representative of a certain level of co-operative behaviour.

It would be interesting to know whether the aggressive responses to a squeal of terror, a "fear-threatening" attitude, and a hostile attack, are innate or socially conditioned. At present there are no available data bearing directly on this question, but other facts go to show that they are mainly unconditioned reactions.

The "blind" and reflex character of many social responses of sub-human primates is demonstrated by the fact that these animals do not distinguish between the dead and the living. That is to say, a variety of social responses may be equally stimulated by either living or dead animals, in spite of the meaningless nature of responses evoked by the dead. Thus, monkeys do not limit their rescue activities to their living companions; they also refuse to leave those that

are dead. Sir Harry Johnston [208] relates how he once killed a baboon in Caga—one of a troop that was plundering a maize plantation. Instead of running away, its fellows surrounded the corpse and refused to let him approach. It was not before he had returned with several of his followers that the baboons ran off, and he was able to recover the dead one. Similar behaviour is exhibited whenever it is necessary to remove a dead body from Monkey Hill in the London Zoological Gardens. The remaining baboons try to prevent the abduction of the body as if it were a living animal. Apes behave in a comparable way. Brown [55A] relates how one chimpanzee "violently opposed" the removal of its dead companion. Such behaviour clearly suggests a lack of apprehension, on a social level, of the significance of death. The same lack of distinction between the dead and living is certainly manifested on a sexual level. When a female baboon dies in a "sexual fight" on Monkey Hill, the males continue to quarrel over her dead body, which they also use as a sexual object until it is forcibly removed by the keepers. Usually the removal demands much strategy and subterfuge in order to circumvent the vicious attacks of the dead female's companions, and sometimes two days may pass before the keepers succeed in their object. A similar failure to distinguish between the dead and the living is shown in the mutual responses of a mother and her child. Thus, when a nursing sub-human primate is shot, her baby clings to her body and is removed only with difficulty, squealing and making anxious struggles to return to the corpse. A very large number of the monkeys and apes that come into captivity are the babies caught in this way. Not only do young monkeys and apes cling to their dead mothers, but the reverse also occurs—the mother clings to her dead baby, which she refuses to surrender. This has been repeatedly recorded. All the baboon babies that have died on Monkey Hill in the London Zoological Gardens have, without

exception, been retained by their mothers until forcibly removed. The greatest difficulty faced the keepers in their attempts to secure the bodies of these young animals, and few have been recovered.

The obvious implication of these facts is that sub-human primates have no real apprehension of the social situations of which they themselves form part. A specific situation evokes a characteristic response which does not vary until the stimulus changes. Hence the use of the term "blind response" with reference to their seemingly co-operative social reactions.

The retention of the dead baby by a nursing sub-human primate is usually interpreted as representing an overflow of maternal sentiment or maternal instinct. This is the implication of a paper by Yerkes [388] entitled "Maternal Instinct in a Monkey". The paper concerns the behaviour of a hybrid Rhesus and common macaque to her still-born baby, which she refused to surrender, carrying it with her wherever she moved. The father was also interested, and together with her spent much time picking over the dead baby, the two frequently examining the eyes "as if in attempts to open them". Observations were made from day to day, and every opportunity was sought to remove the body, but without success. At the end of the second week the corpse was so far decomposed by the constant handling and licking of the adults that it rapidly wore away. By the third week there remained only some shrivelled skin covering a few fragments of bone, including the skull which had been opened. The remnant became smaller and smaller, and disappeared about five weeks after the birth. Yerkes' interpretation is that

> "during a period of five weeks the instinct to protect her offspring impelled this monkey to carry its gradually vanishing remains about with her and to watch over them so assiduously that it was utterly impossible to take them from her except by force."
>
> "After reading this note in manuscript, Dr. Hamilton informed me that Gertie had behaved towards her first still-

birth as toward her second. And, further, that Grace, a baboon, also carried a still-birth about for weeks. I am now heartily glad that my early efforts to remove the corpse were futile, for this record of the persistence of maternal behaviour seems to me of very unusual interest to the genetic psychologist."

Numerous opportunities have arisen for similar observations on Monkey Hill. The facts suggest that Yerkes' interpretation is only a partial explanation of the behaviour of the mother, unless the term "maternal behaviour" is very loosely defined. When the data are analysed, they suggest that the retention of the body is immediately due to the continued operation of maternal responses, but that it is fundamentally the monkey's reaction to a furry object.

When a nursing monkey's baby dies her behaviour towards it is at first identical with her responses during its lifetime. No change occurs in the manner in which she holds it. She presses it to her breast, and carries it in her arms wherever she goes. At first she never puts it down, picking through its fur as she did when it lived. She examines its mouth and its eyes, its nose and its ears. In a few days one notices a change in her behaviour. A slightly decomposing body now droops over her arms. Except when moving, she no longer presses it to her breast, and although she continues to groom the body and to bite at the skin, she begins to lay it on the ground more frequently. The body becomes yet more decomposed, and mummification sets in, but her investigation of the skin and fur continues. The dried-up body now begins to disintegrate. One notices a leg missing, an arm missing, and it is soon, as Yerkes wrote, a shrivelled bit of skin. The mother is more often seen biting off pieces—it is unknown whether she swallows them. At about this stage she may abandon of her own accord what is left of the shrivelled remains.

Before discussing the significance of this sequence of events, certain complementary facts may be noted. It is

PLATE XXIV

Photograph by F W Bond

A FEMALE BABOON, WITH HER DEAD BABY IN HER ARMS, BEING GROOMED BY HER OVERLORD

(See p. 300)

face p 300

reported that the bachelor baboon who strangled a baby dropped by a nursing baboon during the course of a fight on Monkey Hill,* carried the corpse with him for a week before it was rescued by the keepers. Many kinds of furry and feathery objects are often retained by sub-human primates. A year-old baboon under my own observation seized a young kitten, killed it, and retained the body throughout the day, protesting vigorously when it was removed from her in the evening. During the day she carried it closely in her arms and picked through its fur. Monkeys can be seen from time to time in the London Zoological Gardens picking through the feathers of sparrows they have killed. Loveridge [239A] has recorded his observations of the behaviour of a captive Cercopitheque to whom the warm body of a recently killed rat was thrown.

> "First seizing the tail in her mouth she defied anyone to take it from her, then she subjected it to a critical examination, opening the mouth and looking inside, licked the blood from its nose, examined its fur minutely and appeared to capture and eat some fleas which she found there. After this she climbed to her box upon which she sat and placing the rat between her knees nursed it in a most comical way. She clung to this rat for two days, defeating every effort to deprive her of it; by the end of this time all the fur was off, the carcase was positively green and liquid, and as she held it in her mouth the flies buzzed all about her."

When these facts are considered in relation to the behaviour of a nursing monkey who retains the body of her dead offspring, it becomes obvious that her actions are not interpreted by the phrase "persistence of maternal behaviour". They could in large part be explained as the operation of a response common to females of apparently all ages as well as to males, and one for which the significant stimulus can be greatly altered—from monkey baby to dead rat—without effectively altering the character of the response. This common response obviously cannot be called

* See p. 222.

maternal. It represents a situation in which there are two poles—the one, a living animal completely positive or dominant; the other, a dead body, completely negative or submissive.

One cannot gauge the extent to which the behaviour of a mother monkey "nursing" her dead offspring inclines from the common "living-dead" response to the genuine maternal behaviour of a nursing monkey. Only one consideration suggests that it does incline in that direction. This is that for the first few days after the death of her baby the mother continues in the physiological state of lactation. Physiological forces impel her towards the continuation of a social situation to which she is already conditioned; they impel her to carry on pressing her dead baby to her functioning breasts. Thus her overt behaviour for the first few days after the death of the infant corresponds closely with the mother's part in the overt behaviour of nursing. The evidence does not suggest that the maternal element in her total responses to the dead baby is great. It does indicate that the later phases of her reactions to the dead infant consist essentially in the "living-dead" relationship manifested by all primates.

This analysis of "living-dead" relationships perhaps throws some light upon the problems raised by the "living" relationships of sub-human primates. Thus, one may consider that three factors contribute to effective maternal behaviour. The two primary factors are fundamentally of social significance, and are firstly, the mother's attraction to a small furry object, and secondly, the strong attraction of the living baby to its mother's fur. The third factor—which gives the maternal response its obvious significance—is the sucking reflex of the young animal, which in its operation relieves a state of mammary tension in the mother. When the baby dies, and the mammary glands cease functioning, the significance of the relationship becomes purely social, and consists only of the mother's response to a small furry object.

The sexual relationship also achieves a new significance in the light of these facts. The adult female is a stimulus which evokes characteristic socio-sexual responses in the male. It is only in the absence of the female's responses that the sexual situation of a living male and a dead female at first differs from the comparable situation that contains a living female. When the intensity of such a situation is increased by the interest of other males in the dead female, the responses of the temporary owner of the body immediately become stronger. He maintains his hold more fiercely, and he uses the carcase as a sexual object more frequently. The moment he has driven away his interested fellows, his own interest in the body seems to decline.

The sexual bond is stronger than the social relationship, and an adult male, unlike a female, is not owned by any individual fellow. Moreover, he is not a small furry object that can be picked up and carried. His social relationships are thus mainly concerned with grooming, and are dependent upon his own active participation. The only situation in which he need not actively direct his responses towards his fellows, in order to secure their attention, is one in which he is attacked by something outside his group. The resentment of monkeys at the removal of a dead male body is the same resentment they show when attempts are made by some individual outside their group to remove or attack any of their living fellows.*

* It is interesting to speculate about the final response in the whole pattern of behaviour connected with the retention of the dead. Numerous observers have recorded their appreciation of the taste of monkey flesh. For example, Rengger [293] appends to his systematic description of many species of South American monkey a reference to the taste of the flesh of the species. Sir Harry Johnston [208] writes with reference to a baboon he roasted, "the succulence and quality of this creature's flesh were quite unexceptionable". The possibility arises that monkeys and apes may also sometimes eat and enjoy their dead. There is a certain amount of evidence for such a view. Thus, the mother monkey appears to eat pieces of her dead baby, and Anderson states that he "can vouch for the fact that a male *Hylobates leuciscus*, Schreber,

Three conclusions have emerged from this discussion of the purely social relationships of sub-human primates. The first is that the response to fur is a fundamental factor in social behaviour. The second is that such behaviour as might superficially come under the heading of "mutual aid" is reflex in character. The third and perhaps most striking fact is that sub-human primates do not distinguish in their reactions between the living and the dead. That is to say, they have no appreciation of death.

The immediate reaction of the new-born baby to fur, which is obviously an unconditioned reaction, was emphasized in an earlier chapter. Its importance is perhaps demonstrated by the fact that a young primate maintains its hold on its mother's fur after her death, and that it apparently is not specifically attracted to her body since, as the observations recorded on page 204 indicate, it is equally soothed by the carcase of any dead baboon.* The fundamental nature of the reaction to fur is perhaps also indicated by its ill-defined character and by the variety of situations in which it is evoked. Feathers, brooms, mice, kittens are all adequate stimuli. It seems very likely that the social performance of grooming develops from this innate response to fur, and that it always remains one of the fundamental bonds holding sub-human primates together.

The reflex character of the reaction of a monkey who rushes to the aid of a tormented fellow has been emphasized sufficiently not to require summarizing here. Its "blind" character is demonstrated by the fact that the monkey responds in the same way to an "assault"

robbed a female *Semnopithecus pileatus*, Blyth, of her babe, killed it and partially ate it. The incident occurred in the Calcutta Zoological Gardens on the 6th May, 1877."[27] It is conceivable, therefore, that the sub-human primates assist the scavengers of the animal world by eating their dead fellows. The remains of monkeys and apes are very rarely found in the wild.

* A farmer whom I met took advantage of this fact by providing young baboons he reared with a piece of the cured hide of a baboon, to which the young animals clung and were thus comforted.

upon a dead companion. Monkeys and apes do not recognize death, for they react to their dead companions as if the latter were alive but passive. Thus the "blind" character of their social responses would seem to deny them any claim to altruism.

CHAPTER XIX

THE SOCIAL SCALE

AN immature Rhesus monkey called Cupid, living in the Psychology Laboratory of the University of California, became attached to Psyche, a female common macaque much older than himself. At first he was completely dominated, and a fortnight had passed before he was seen to respond to her repeated presentations by mounting. During the following year he grew until he was bigger and stronger than the female, and about the end of this time the two animals had assumed mature and normal mating relations. Two and a half years after their first meeting, two young female Rhesus monkeys, Eva and Topsy, were introduced into the laboratory, the male proving very antagonistic to their intrusion. When they were introduced into his cage—Psyche having been previously removed—he attacked both of them viciously, and when they were taken away, he greeted the return of his old female with conspicuous sexual interest. The recorder of this tale, Tinklepaugh,[357] to whom the animals belonged, failed to bring about a conciliation between the male and the younger females, for it attacked them even after it had been sexually starved by isolation for two to three weeks. Thus he received the impression that Cupid had built up "what was virtually a monogamous attachment for Psyche." About nine months after the young animals had been introduced to the male, Tinklepaugh made strong efforts, by feeding and muzzling, to induce Cupid to enter into relationship with Topsy. About a fortnight passed before the male's antagonistic attitude was effectively replaced by one of attraction. Five days after friendly

relations had been established, Topsy was removed from the cage, and his old mate, Psyche, reintroduced. Cupid's attitude to Psyche was normal, although sexual responses were not so frequently displayed as before their separation. He spent much time gazing at Topsy who had been placed in an adjacent cage. A fortnight later Psyche was again removed and Topsy in turn reintroduced. Cupid mounted her, but immediately jumped away and began to bite his hind feet, an action that had been part of his play from his earliest days in the laboratory. Such behaviour was noted many times during the first three days after their reunion, but he was never seen to complete the sexual act. This part of the story is best told in Tinklepaugh's own words:

> "On the fourth day he was discovered with his hind feet rather badly lacerated. To facilitate examination and medical attention, he was led from his cage by the doorway leading into the area between it and the nearby cage now containing Psyche and Eva. He looked back at the cage where Topsy still remained and then toward the cage containing the other two females. Psyche, who had seemed to be much upset by Topsy's presence in Cupid's cage, was now on the side of her cage shrieking threateningly across at the other female. Suddenly, and with no previous signs of anger or particular emotion, Cupid lurched to the end of his chain and began to bite himself. In a few seconds he tore huge jagged rents in his already lacerated legs. Then, as though in intense pain, he jumped into the writer's arms."

After Cupid's wounds were dressed, he was placed in his cage and Psyche was returned to him "to nurse his wounds—a task she performed remarkably well—and also because it was believed that her presence would have a quieting effect upon him." Cupid soon recovered and after about three weeks resumed normal sex relations with Psyche, although he remained "in a state comparable to the depression of some psychoses." He sat about quietly for hours and was highly irritable, and when excited he seized and bit his

healing legs. This action was evoked particularly when Tinklepaugh directed his gaze towards the monkey or spoke to it. Such behaviour continued for months and was repeated even after an interval of eight weeks during which Tinklepaugh had not visited his monkeys. Deciding, therefore, that the tendency of the animal to mutilate itself whenever he looked at it could not be effaced by time alone, he finally whipped the monkey and in this way effectively inhibited its "masochistic" activities. Fourteen months after the first incident of self-mutilation, Cupid was living a normal sex life, his mates being Psyche and Eva, Topsy having died. Even at this time he still seized his hind feet in his teeth when excited, biting them gently.

Tinklepaugh declares that he places no interpretation upon Cupid's behaviour, but simply "presents sufficient details so that the reader can formulate his own conclusions." He labels his description, however, with the statement that it "deals with the self-mutilation of a male monkey after he had formed what was evidently a monogamous attachment for a female of a different species and then had another female of his own species introduced into the situation." There is thus sufficient interpretation in the opening sentence of the description for one to understand the way in which Miller [258] refers to it in his discussion of the sexual behaviour of primates. The implication Miller naturally makes is that the "socially effective sentiment of love", a significant feature of human society, is probably foreshadowed in the behaviour of the monkey Cupid. Before this implication is definitely accepted, it is as well to examine the story in greater detail.

An immediate question that demands examination is whether Tinklepaugh had any justification for his opinion that the monkey had formed a monogamous attachment for Psyche. The evidence upon which he based the statement has been quoted. Cupid had attacked the young females on five successive occasions when they were introduced into his cage, even though

he had been sexually starved for two to three weeks before three of these incidents. When Psyche was returned he continued to manifest a strong sexual interest in her. However, it only required a fortnight's conditioning, for the first ten days of which the animals were separated by a wire partition, before Cupid was on sexual terms with Topsy; and only two to three weeks, during which he remained antagonistic towards Eva, passed before he accepted her, too, both socially and sexually. Thus, at the very best, Cupid's "monogamous feeling" towards Psyche was not of a durable kind. There is doubt, however, of its reality, for his initial behaviour to the young animals may have had no connection with his social adaptation to Psyche. Indeed, his actions were typical of the attitude that a more dominant monkey may assume when new animals are introduced into its immediate environment, and his may have been a display of dominance rather than of sexual antagonism. There remains, however, the question of his "masochistic" attacks upon himself. An obvious anthropomorphic interpretation is that they were induced by the conflict of his attractions to the two female monkeys. This may be true, and in that case there is perhaps some justification for the view that the monkey definitely was attached to Psyche. On the other hand, there is evidence that makes one distrust the anthropomorphic point of view. From Tinklepaugh's description, Cupid had manifested these attacks of self-mutilation for about two years before they became serious, even while he was still alone with Psyche. Moreover, they did not cease when he had become sexually readjusted to Psyche after his serious attack upon himself. Unless, therefore, one is prepared to stretch the point very far, and to assume that he had suffered some lasting psychological trauma from the conflict of his sexual attractions, there does not appear to have been any close correlation between the monkey's practice of self-mutilation and his sexual activities. Such a view is strengthened by the fact

that these attacks of self-mutilation are very common amongst caged monkeys of almost all species. At the time of writing it is very frequently manifested in the London Zoological Gardens, both by the male of a pair of Japanese monkeys and by an adult female pig-tailed monkey. The Japanese monkeys are confined together, in a cage that is separated by a wire partition from an adult pig-tailed monkey on one side and an adult Gibraltar ape on the other. The male's relationships with his neighbours are, if anything, antagonistic, and he may often be seen lunging with dominant thrusts at the separating partitions. There is no obvious conflict of attraction to explain the many occasions on which this Japanese monkey seizes a foot in its mouth, contorting its body into an awkward shape, the while it dances round on one foot, biting the other. It is difficult to say what is the significance of such behaviour. There is no obvious justification for the view expressed by Tinklepaugh that it is exhibitionistic. There is also very little reason to explain why the female pig-tailed monkey behaves in this way. Sometimes her contortions appear to be a manifestation of rage inspired by onlookers, sometimes they seem to be the result of irritation induced by the play of her young infant, sometimes they have no obvious predisposing cause. But such "masochistic" attacks may well be a reaction to the inhibition of a natural dominant display. Thus, to give an example, at the moment when the monkey Cupid attacked itself it was restrained, by Tinklepaugh, and so was unable to participate in a situation in which one of two animals it habitually dominated was shrieking threateningly at the other. The pig-tailed monkey in the London Gardens similarly attacks herself when, owing to the wire partition, she cannot more adequately release her hatred for certain habitual human visitors whom she greatly dislikes. That these attacks of self-mutilation represent referred assaults is practically proved by the fact that they are provoked when either the Japanese ape or the pig-tailed

monkey is tormented. After some minutes spent in vain thrusts at the wires these animals suddenly transfer their aggressive activities to themselves. Thus, when all the possibilities are considered, it becomes difficult to associate the "masochistic" behaviour of Cupid with a monogamous attitude for which no other evidence has been submitted.

But evidence can be cited to show that sub-human primates do form relatively permanent affective social relationships. Facts have been recorded in preceding pages which demonstrate that such relationships are manifested between particular males of the same age and of different ages in the Hamadryas baboon colony. They are also displayed by differences in the attitude of an overlord to the respective females of his harem. Such differences in heterosexual interest are clearly the result of "temperamental" differences between the females. In one observed case a more assertive and dominant female maintained closer relations with her overlord than did one who was completely subjugated. Such contrasts in the underlying attitude of the overlord to the females of his harem are, however, completely outweighed by his responses to their varying physiological conditions of heat. The female who is completely subjugated will take a prior place in the harem when her sexual skin is swollen. This fact does not encourage a belief in monogamous tendencies. Moreover, taken together with our knowledge of the manner in which males secure females by conflict, it strongly suggests that sexual selection, as defined by Darwin, has no important place in the social mechanisms of those sub-human primates whose behaviour is known. Affective sentiments may exist, but they are not necessarily linked with sexual relationships.

If his views on the absence of heat periods are disregarded, one can accept Miller's statement that "so far as they have been recorded in the laboratory the main features of simian sexual tendencies tally with well known elements in human behavior,"

From the evidence discussed in earlier chapters, one can go even further and say that under natural conditions, in the wild, the sexual activities of sub-human primates still show great similarity to human tendencies.

Since the sexual activities of monkeys correspond overtly with human responses, it may be asked whether they necessarily have the same social significance. When the observed facts are analysed, the sexual activities of sub-human primates are found to differ from those of man in their social significance, mainly by their lack of what may be called definition.

In human society children are differentiated from adults in all socio-sexual situations; homosexual behaviour is significantly distinguished from heterosexual behaviour; social relations with the living are clearly demarcated from social relations with the dead. If these distinctions are not naturally apprehended, they are at any rate enforced by the law. That is to say, though they may not be determined by biological factors, they are distinctions that are valid on a cultural level. But in the monkey, sexual activities are primarily diffuse in character. Sexual responses develop early in life and then become expressed in an extravagantly varied manner within a social system based on dominance. Every animal obtains such social and material advantages as he can in a predominantly hostile environment. Except in some situations of attack, it is usually every monkey for himself. If one monkey quarrels with a weaker fellow, he must beware lest an even stronger member of his group set upon him. If one secures the only piece of fruit in his neighbourhood, he must watch lest it be snatched away by a stronger animal. An adult male may be only dominant enough to secure one female; a fellow may secure six. In all situations the position an animal holds in relation to its fellows is the outcome of the interaction of its own dominant qualities with those of the other members of its group. Monkeys, both male and female, are adapted to such a social system partly through sexual

reactions. A weaker animal assumes the female sexual attitude before a more dominant fellow. A comparatively dominant animal assumes the male attitude to those below it in the scale of social dominance. Thus a female who at one moment has submitted to the sexual approach of her overlord, may at the next mount in the male position another female, an immature male, or a submissive male belonging to her party. A young animal that she has mounted may immediately cover a still more submissive animal. The overlord who has just covered one of his females may, a moment later, assume the female position to another male. A mother who is nursing her child may, in other cirsumstances, incite it to cover her. The dead are used as sexual objects, and are sought after by their former fellows. Thus in the life of a sub-human primate there is not the same clean-cut distinction between male and female, between young and old, between living and dead, between homosexuality and heterosexuality, or even between monogamy and polygyny as there is in human society. This is a fundamental difference and, implying as it does that sub-human primates do not apprehend in the way man does the significant characters of different social relations, it reflects the very wide gap separating the intelligent activities of man from those of other primates.

The overt socio-sexual activities of sub-human primates are much further removed from those of the lower mammal than from those of man. The factors underlying associations of monkeys and apes are characterized by their continuous, rather than intermittent, sexual nature. The male primate is always sexually potent, while the female is also always to some extent receptive. In the lower mammal, on the other hand, the female, as a rule, accepts the male only during isolated periods of heat, and this intermittent character of the sexual bond is reflected in the transitory nature of their social unions. Moreover the sexual responses of the lower mammal are mostly unconditioned and have

but a small range of variation. Those of the primate, on the other hand, develop within the environment of a complex society and become largely conditioned; hence their greater variability. In the primate three factors may theoretically be regarded as underlying the release of sexual responses from strict physiological control. The first of these is the nature of the primate reproductive mechanism itself, which differs from that of a typical lower mammal in that although periods of increased stimulation do occur, they are not sharply defined; to some extent the physiological sexual stimulus is always present. The second and third factors are in a sense linked. Anthropomorphically one may describe them by saying that the sensori-motor equipment and "intelligence" of the monkey is such that he is able to take advantage of the permanent sexual association in which he lives to engage in sexual activities that are not directly associated with reproductive function or with sexual satisfaction. The sub-human Old World primate may be said to prostitute its sex in a social life that is built upon the principle of dominance. Under ordinary conditions the sexual stimulus is stronger than most other stimuli that determine common forms of response, and it is able to outweigh them if it becomes effective during the period of their operation. Thus a stimulus that has determined aggressive behaviour in a monkey may be outweighed and the aggression diverted if the animal is presented with a stimulus of a sexual nature. It is clear then that, anthropomorphically speaking, it is by means of its sex that a monkey is able to obtain advantages to which it is not entitled by its position in the scale of dominance of its group. Such "prostitution" is unknown in the life of the lower mammal.

The nucleus of the societies of monkeys and apes is the family party, consisting of an overlord and his harem, held together primarily by the interest of the male in his females and by their interest in their young. Paternal interest is not strongly manifested

by sub-human primates, and in this they doubtless show resemblances to the behaviour of the lower mammals. But the family of the primate differs from that of the lower mammal, since one of its essential members is the overlord. The male of most lower mammals separates from his females after his rutting season is past, so that the family in his species is formed by the female and her young. A conspicuous characteristic of the harem system and the system of dominance in the primates is the absence of all but clandestine promiscuity. And in this again the primate differs from many lower mammals. The harem forms the nucleus when several family parties unite to form a larger herd, but the herd never appears to be so stable a unit as the family, which never loses its identity within the larger group. Contrary to Miller's belief, there are no "loosely organized or sexually promiscuous" bands of monkeys and apes.

In this book an attempt has been made to present some of the conspicuous facts of sub-human primate social life. As was stated in an introductory chapter, one may see in the life of the monkey a crude picture of a social level from which emerged our earliest human ancestors some time in the first half of the Tertiary geological epoch. Since few significant differences can be seen between the broader social mechanisms of different monkeys and apes, and since man is also an Old World primate, one may assume that the social level discussed in this book is one through which man passed in the pre-human stages of his evolution. Nothing is known of intermediate social levels that may have existed between that of the sub-human primate and that of the most primitive food gatherer ever described. At the one extreme there is the monkey or ape with its harem, frugivorous, without any vestige of cultural processes. At the other extreme is man, usually monogamous, omnivorous, whose every activity is culturally conditioned. Socially there are no obvious

comparisons between man and the ape. Familially there are perhaps some. The permanent sexual association of human beings is a characteristic common to all primates, and one that is not manifested by the majority of lower mammals. But the family unit in man differs from that of the sub-human primate. At its lowest level, according to most authorities, the family of human society was monogamous. If reason played a part in determining the nature of the human family unit, it is very probable that it was guided by the demands of man's omnivorous diet. The polygynous gorilla or baboon can guard his females from the attentions of other males while they all forage together for fruits and young shoots. Primitive man, who, as his Paleolithic arts display, was an animal largely dependent upon a diet of meat, would not have gone hunting if in his absence his females were abducted by his fellows. Reason may have forced the compromise of monogamy.

BIBLIOGRAPHY

1. ADAMS, D. K. 1929. Experimental Studies of Adaptive Behavior in Cats. *Comp. Psych. Monographs*, Baltimore, Vol. 6, pp. 1–168.
2. AKELEY, CARL E. 1922. Hunting Gorillas in Central Africa. *World's Work*, New York, Vol. 44, pp. 169–183, 307–318, 393–399, 525–535.
3. ——— 1923. *In Brightest Africa*. New York.
4. ——— 1923. Gorillas, Real and Mythical. *Journ. Amer. Mus. Nat. Hist.*, New York, Vol. 23, pp. 428–447.
5. Akeley Memorial No. of *Journ. Amer. Mus. Nat. Hist.*, New York, Vol. 27, 1927, p. 168.
6. ALLEN, EDGAR. 1926. Progress of Work on the Mechanism of the Menstrual Cycle of the Monkey, *Macacus rhesus*. *Anat. Rec.*, Philadelphia, Vol. 32, p. 226 (Abstract).
7. ——— 1926. The Time of Ovulation in the Menstrual Cycle of the Monkey, *Macacus rhesus*. *Proc. Soc. Exp. Biol. & Med.*, New York, Vol. 23, pp. 381–383.
8. ——— 1926. The Menstrual Cycle in the Monkey: Effect of Double Ovariectomy and Injury to Large Follicles. *Proc. Soc. Exp. Biol. & Med.*, New York, Vol. 23, pp. 434–436.
9. ——— 1927. The Menstrual Cycle of the Monkey, *Macacus rhesus*: Observations on Normal Animals, the Effects of Removal of the Ovaries and the Effects of Injections of Ovarian and Placental Extracts into the Spayed Animals. *Contributions to Embryol.*, Washington, 98, Vol. 19, pp. 1–44.
10. ——— 1928. Effects of Ovariectomy upon Menstruation in Monkeys. *Amer. Journ. Physiol.*, Baltimore, Vol. 85, pp. 471–475.
11. ——— 1928. Sex Characteristics in Monkeys. *Proc. Soc. Exp. Biol. & Med.*, New York, Vol. 25, pp. 325–327.
12. ——— 1928. An Unfertilized Tubal Ovum from *Macacus rhesus*. *Anat. Rec.*, Philadelphia, Vol. 37, pp. 351–356.
13. ——— 1928. Further Experiments with an Ovarian Hormone in the Ovariectomized adult Monkey, *Macacus rhesus*, especially the Degenerative Phase of the Experimental Menstrual Cycle. *Amer. Journ. Anat.*, Philadelphia, Vol. 42, pp. 467–486.

14. ALLEN, EDGAR. 1928. Reactions of Immature Monkeys (*Macacus rhesus*) to Injections of Ovarian Hormone. *Journ. Morph. & Physiol.*, Boston, Vol. 46, pp. 479–495.

15. ALLEN, E., MADDUX, W. P., and KENNEDY, J. W. 1931. Ovarian and Anterior Pituitary Hormones from the Pregnant Monkey. *Proc. Soc. Exp. Biol. & Med.*, New York, Vol. 28, pp. 403–404.

16. ALLEN, G. M., and LOVERIDGE, A. 1927. Mammals from the Uluguru and Usambara Mountains, Tanganyika Territory. *Proc. Boston Soc.*, N.H., Vol. 38, pp. 413–441.

17. ALLEN, J. A. 1916. Mammals Collected on the Roosevelt Brazilian Expedition, with Field Notes by Leo E. Miller. *Bull. Amer. Mus. Nat. Hist.*, New York, Vol. 35, pp. 559–610.

18. ALLEN, W. M. 1930. Physiology of the Corpus Luteum. V. The Preparation and some Chemical Properties of Progestin, a Hormone of the Corpus Luteum which produces Progestational Proliferation. *Amer. Journ. Physiol.*, Baltimore, Vol. 92, pp. 174–188.

19. ——— 1930. Physiology of the Corpus Luteum. VI. The Production of Progestational Proliferation of the Endometrium of the Immature Rabbit by Progestin (an Extract of the Corpus Luteum) after Preliminary Treatment with Oestrin. *Amer. Journ. Physiol.*, Baltimore, Vol. 92, pp. 612–618.

20. ——— 1931. Cyclical alterations of the endometrium of the rat during the normal cycle, pseudo-pregnancy, and pregnancy. Production of deciduomata during pregnancy. *Anat. Rec.*, Philadelphia, Vol. 48, pp. 65–91.

21. ALLEN, W. M., and CORNER, G. W. 1929. A Hormone of the Corpus Luteum, producing Progestational Proliferation of the Uterus. *Anat. Rec.*, Vol. 42, p. 3 (Abstract).

22. ——— 1930. Physiology of the Corpus Luteum. VII. Maintenance of Pregnancy in Rabbit after very early castration, by Corpus Luteum Extracts. *Proc. Soc. Exp. Biol. & Med.*, New York, Vol. 27, pp. 403–405.

23. ALLESCH, G. J. VON. 1921. Geburt und erste Lebensmonate eines Schimpansen. *Naturwissenschaften*, Berlin, Bd. 9, pp. 774–776.

24. ALVERDES, FR. 1927. *Social Life in the Animal World.* Kegan Paul, Trench, Trübner & Co., Ltd. London.

25. ANDERSON, J. 1878. *Anatomical and Zoological Researches in Western Yunnan.* Vol. 1. Quaritch. London.

26. ——— 1883. *Guide to the Calcutta Zoological Gardens.* Calcutta.

27. ——— 1902. *Zoology of Egypt.* Revised and completed by W. E. de Winton. Hugh Rees. London.

28. ANTONIUS, O. 1929. Eine Beobachtung an Affenkastraten in Schönbrunn. *Zoolog. Garten*, Leipzig, N.F. Band 2, Heft 4/6, pp. 134–135.

29. ASCHEMEIER, C. R. 1921. On the Gorilla and Chimpanzee. *Journ. Mamm.*, Baltimore, Vol. 2, pp. 90–92.

29A. ——— 1922. Beds of the Gorilla and Chimpanzee. *Journ. Mamm.*, Baltimore, Vol. 3, pp. 176–178.

30. AVERY, G. T. 1925. Notes on Reproduction in Guinea-pigs. *Journ. Comp. Psych.*, Baltimore, Vol. 5, pp. 373–396.

31. BAKER, J. R. 1930. The Breeding-Season in British Wild Mice. *Proc. Zool. Soc.*, London, pp. 113–126.

32. BANKS, E. 1929. Interbreeding among some Bornean Leaf Monkeys of the Genus *Pithecus*. *Proc. Zool. Soc.*, London, pp. 693–695.

33. BANTA, A. M. 1914. Sex Recognition and the Mating Behaviour of the Wood Frog, *Rana sylvatica*. *Biol. Bull.*, Wood's Hole, Mass., Vol. 26, pp. 171–184.

34. BARNS, T. A. 1922. *The Wonderland of the Eastern Congo*. G. P. Putnam. London and New York.

35. ——— 1923. *Across the Great Craterland to the Congo*. Ernest Benn. London.

36. BARTLETT, E. 1871. Notes on the Monkeys of Eastern Peru. *Proc. Zool. Soc.*, London, pp. 217–220.

37. BATES, H. W. 1895. *The Naturalist on the River Amazon*. John Murray. London.

38. BELLERBY, C. W. 1929. Ovulation produced by Anterior Lobe. *Journ. Physiol.*, London, Vol. 67, p. xxxiii.

39. BINGHAM, HAROLD C. 1927. Parental Play of Chimpanzees. *Journ. Mamm.*, Baltimore, Vol. 8, No. 2, pp. 77–89.

40. ——— 1928. Sex Development in Apes. *Comp. Psych. Monographs*, Baltimore, Vol. 5, pp. 1–161.

41. ——— 1929. Selective Transportation by Chimpanzees. *Comp. Psych. Monographs*, Baltimore, Vol. 6, pp. 1–45.

42. ——— 1929. Observations on Growth and Development of Chimpanzees. *Amer. Journ. Phys. Anthrop.*, The Wistar Institute Press, Philadelphia, Vol. 13, pp. 433–468.

43. ——— 1929. Chimpanzee Translocation by Means of Boxes. *Comp. Psych. Monographs*, Baltimore, Vol. 5, No. 3, pp. 1–91.

44. BINGLEY, The Rev. W. 1824. *Animal Biography*, Vol. 1. London.

45. BLANFORD, W. T. 1870. *Geology and Zoology of Abyssinia*. MacMillan. London.

46. ——— 1888–1891. *The Fauna of British India*. Part I, Mammalia. Taylor and Francis. London.

47. BLYTH, E. 1843. *Remarks on the Zoology of the Tenasserim Provinces.* Calcutta.

48. BOUTAN, L. 1913. Le Pseudo-Langage. Observations effectuées sur un Anthropoïde : le Gibbon. *Actes Soc. Linn.*, Bordeaux, Vol. 67, pp. 5–79.

49. BRADLEY, MARY HASTINGS. 1922. *On the Gorilla Trail.* New York.

50. BRANDES, G. 1930. Wichtige Daten über das Heranwachsen des Gorilla. *Der Zoolog. Garten.*, Leipzig, Bd. 3, pp. 104–116.

50A. ——— 1931. Wie alt wird der Orang-Utan? *Zool. Garten*, Leipzig, Vol. 4, pp. 1–9.

51. BREHM, A. E. 1922. *Die Menschenaffen.* Leipzig. Pp. 148.

52. BRESCHET, G. 1845. Recherches Anatomiques et Physiologiques sur la Gestation des Quadrumanes. *Mem. Acad. Sci.*, Paris, Tome 19, pp. 401–490.

53. BRIFFAULT, R. 1927. *The Mothers.* Vol. 1–3. Allen & Unwin. London.

54. BROOKE, J. 1841. Letter on the Species and Distribution of Orangs. *Proc. Zool. Soc.*, London, pp. 55–61.

55. BROWN, A. E. 1878. Fear of Monkeys for Snakes. *Amer. Nat.*, New York, Vol. 12, pp. 225–228, 554–556.

55A. ——— 1879. Grief in the Chimpanzee. *Amer. Nat.*, New York, Vol. 13, pp. 173–175.

55B. ——— 1883. The Kindred of Man. *Amer. Nat.*, New York, Vol. 17, pp. 119–130.

56. BUFFON, COMTE DE. 1775. *Natural History.* Translated by W. Kendrick and J. Murdoch. Vol. 3 and Vol. 4. T. Bell. London.

57. BURBRIDGE, B. 1928. *Gorilla.* Harrap. London.

58. BURRELL, H. 1923. The Nest of a Chimpanzee. *Journ. Mamm.*, Baltimore, Vol. 4, pp. 178–180.

59. BURT, W. H. 1928. Additional Notes on the Life History of the Goss Lemming Mouse. *Journ. Mamm.*, Baltimore, Vol. 9, pp. 212–216.

60. BURTON, R. F. 1876. *Two Trips to Gorilla Land and the Cataracts of the Congo.* London.

61. CANDLER, G. 1903. Notes on the Habits of the Hoolock. *Proc. Zool. Soc.*, London, Vol. 1, pp. 187–190.

62. ——— 1903. Notes on Habits of Hoolock. *Journ. Bomb. Nat. Hist. Soc.*, Vol. 15, p. 700.

63. CHASEN, F. N. 1924. Preliminary Account of Mammals of Singapore Island. *Singapore Nat.*, Vol. 4, pp. 76–86.

64. CHORLEY, C. W. 1928. Note on Uganda Gorillas. *Proc. Zool. Soc.*, London, pp. 267–268.

65. CHRISTY, C. C. 1915. The Habits of Chimpanzees in African Forests. *Proc. Zool. Soc.*, London, p. 536.

66. Coffey, W. C. 1918. *Productive Sheep Husbandry*. Philadelphia and London.

67. Cole, H. H., Howell, C. E., and Hart, G. H. 1931. The Changes occurring in the Ovary of the Mare during Pregnancy. *Anat. Rec.*, Philadelphia, Vol. 49, pp. 199–208.

68. Cole, L. W., and Long, F. M. 1909. Visual Discrimination in Raccoons. *Journ. Comp. Neur. & Psych.*, Philadelphia, Vol. 19, pp. 657–684.

69. Collett, R. 1892. On a New Monkey from N.E. Sumatra. *Proc. Zool. Soc.*, London, pp. 613–617.

70. Collings, M. R. 1926. A Study of the Cutaneous Reddening and Swelling about the Genitalia of the Monkey, *M. rhesus*. *Anat. Rec.*, Philadelphia, Vol. 33, pp. 271–278.

71. Corin, J. 1910. *Mating, Marriage and the Status of Woman*. Walter Scott. London.

72. Corner, G. W. 1923. Ovulation and Menstruation in *Macacus rhesus*. *Contrib. to Embryol.* Vol. 15, Carnegie Inst. of Washington, pp. 73–101.

73. ——— 1927. The Relation between Menstruation and Ovulation in the Monkey. *Journ. Amer. Med. Assoc.*, Chicago, Vol. 89, pp. 1838–1840.

74. ——— 1930. The Hormonal Control of Lactation. I. Non-effect of the Corpus Luteum. II. Positive Action of Extracts of the Hypophysis. *Amer. Journ. Physiol.*, Baltimore, Vol. 95, pp. 43–55.

75. Crespigny, C. de. 1872. On Northern Borneo. *Journ. Roy. Geog. Soc.*, London, Vol. 16, pp. 171–183.

76. Crew, F. A. E., and Mirskaia, L. 1930. The Lactation Interval in the Mouse. *Quart. Journ. Exp. Physiol.*, London, Vol. 20, pp. 105–110.

77. Cuvier, G. 1834. *The Animal Kingdom*. Vol. 1. G. Henderson. London.

78. Darwin, C. 1871. *The Descent of Man*. 1901 Edition. John Murray. London.

79. ——— 1876. Sexual Selection in relation to Monkeys. *Nature*, London, Vol. 15, pp. 18–19.

80. ——— 1902. *Variations of Animals and Plants*. John Murray. London.

81. Deanesly, R. 1930. The Corpora Lutea of the Mouse, with Special Reference to Fat Accumulation during the Œstrous Cycle. *Proc. Roy. Soc. London*, B, Vol. 106, pp. 578–595.

82. Deanesly, R., Fee, A. R., and Parkes, A. S. 1930. Studies in Ovulation. II. The Effect of Hypophysectomy on the Formation of the Corpus Luteum. *Journ. Physiol.*, London, Vol. 70, pp. 38–44.

83. DE HAAN, J. A. BIERENS. 1925. Versuche über den Farbensinn der Affen. *Tydschr. Ned. Dierk. Ver.*, Leiden, Vol. 2, No. 19, pp. 71–74.

84. ——— 1925. Der relative Wert von Form und Farbenmerkmalen in der Wahrnehmung des Affen. *Biol. Zentralbl.*, Leipzig, Bd. 45, 727–734.

85. ——— 1925. Experiments on Vision in Monkeys. I. The Colour-sense of the Pig-tailed Macaque (*Nemestrinus nemestrinus* L.). *Journ. Comp. Psychol.*, Baltimore, Vol. 5, pp. 417–455.

86. ——— 1930. Über das suchen nach verstecktern Futter bei Affen und Halbaffen. *Zeitschrift für vergleichende Physiologie*, Berlin, Bd. 11, pp. 630–655.

87. ——— 1931. Die Baukunst eines niederen Affen (*Cebus hypoleucus* Humb.). *Tydschr. der Ned., Dierkunde Vereeniging*, Leiden, 3de Serie, Deel 2, pp. 23–27.

87A. ——— 1931. Werkzeuggebrauch und Werkzeugherstellung bei einem niederen Affen (*Cebus hypoleucus* Humb.). *Zeitschr. f. vergleich. Physiol.*, Berlin, Band 13, pp. 640–695.

88. DE HAAN, J. A. BIERENS, and FRIMA, MARGARETA J. 1930. Versuche über den Farbensinn der Lemuren. *Zeitschr. f. vergleich. Physiol.*, Berlin, Band 12, pp. 603–631.

89. DE JONGH, S. E., und LAQUEUR, E. 1931. Ueber die Ursache der menstruellen Blutung. *Acta Brevia Neerlandica*, Amsterdam, Vol. 1, pp. 35–36.

90. DE VOSS, J. C., and GANSON, R. 1915. Color Blindness of Cats. *Journ. Animal Behav.*, Boston, Vol. 5, pp. 115–139.

91. DIXON, W. E., and MARSHALL, F. H. A. 1924. The Influence of the Ovary on Pituitary Secretion: a probable factor in Parturition. *Journ. Physiol.*, Lond., Vol. 59, pp. 276-288.

92. DRAKE-BROCKMAN, R. E. 1910. *The Mammals of Somaliland.* Hurst & Blackett. London.

93. DRESCHER, K., und TRENDELENBURG, W. 1927. Weiterer Beitrag zur Intelligenzprüfung an Affen (einschliesslich Anthropoiden). *Zeitschr. f. vergleich. Physiol.*, Berlin, Bd. 5, pp. 613–642.

94. DU CHAILLU, P. 1861. *Explorations and Adventures in Equatorial Africa.* John Murray. London.

——— 1866. Second Journey into Equatorial Western Africa. *Journ. Roy. Geog. Soc.*, London, Vol. 36, pp. 64–76.

——— 1867. *A Journey to Ashango Land.* John Murray. London.

95. ELLIOT-SMITH, G. 1926. Vision and Evolution. *West London Medical Journ.*, London, Vol. 31, pp. 97–117.

96. ELLIOT-SMITH, G. 1927. *Essays on the Evolution of Man.* 2nd Edition. Oxford Univ. Press.

97. ——— 1930. New Light on Vision. *Nature*, London, Vol. 125, pp. 820–824.

98. ——— 1930. *Human History*. Cape. London.

99. ELLIOT, D. G. 1912. A Review of the Primates. *Monog. Series. Amer. Mus. Nat. Hist.*, New York, Vols. 1 to 3.

100. ELTON, C. 1927. *Animal Ecology*. Sidgwick and Jackson. London.

101. ——— 1930. *Animal Ecology and Evolution*. Milford. Oxford.

102. ELTON, C., FORD, E. B., BAKER, J. R., GARDINER, A. D. 1931. The Health and Parasites of a Wild Mouse Population. *Proc. Zool. Soc.*, London, pp. 657–721.

103. FEE, A. R., and PARKES, A. S. 1929. Studies on Ovulation. 1. The Relation of the Anterior Pituitary Body to Ovulation in the Rabbit. *Journ. Physiol.*, London, Vol. 67, pp. 383–388.

104. FIELDS, P. E. 1928. Form Discrimination in the White Rat. *Journ. Comp. Psych.*, Baltimore, Vol. 8, pp. 143–158.

105. ——— 1929. The White Rat's Use of Visual Stimuli in the Discrimination of Geometrical Figures. *Journ. Comp. Psych.*, Baltimore, Vol. 9, pp. 107–122.

105A. FINN, F. 1929. *Sterndale's Mammalia of India*. Thacker & Spink. Calcutta and Simla.

106. FISCHER, J. VON. 1876. Aus dem Leben eines jungen Mandril (*Cynocephalus mormon*). *Der Zoolog. Garten*, Frankfurt, Jahr. 17, pp. 116–127, 174-179.

107. FITZSIMONS, F. W. 1919. *The Natural History of South Africa*. Vol. 1, Mammals. Longmans Green. London.

108. FLOWER, S. S. 1899. Note on the Proboscis Monkey, *Nasalis larvatus*. *Proc. Zool. Soc.*, London, pp. 785–787.

109. ——— 1900. Notes on the Fauna of the White Nile and its Tributaries. *Proc. Zool. Soc.*, London, pp. 950-973.

110. ——— 1900. On the Mammalia of Siam and the Malay Peninsula. *Proc. Zool. Soc.*, London, pp. 306–379.

111. ——— 1929. *Vertebrate List*. Vol. 1, Mammals. Zoological Society. London.

112. ——— 1930. Notes on eight Continental Zoological Gardens visited in 1929. *Proc. Zool. Soc.*, London, pp. 659–669.

113. ——— 1931. Contributions to our knowledge of the duration of Life in vertebrate Animals. V. Mammals. *Proc. Zool. Soc.*, London, pp. 145–234.

114. FORBES, H. O. 1885. *A Naturalist's Wanderings in the Eastern Archipelago*. Sampson Low, Marston, Searle, & Rivington. London.

115. FORBES, H. O. 1894. *Handbook to the Primates.* Allen. London.

116. FOX, H. 1929. The Birth of Two Anthropoid Apes. *Journ. Mamm.*, Baltimore, Vol. 10, pp. 37–51.

116A. FREUD, S. 1925. *Three Contributions to a Theory of Sex.* Translated by A. A. Brill. Nervous and Mental Disease Monographs Series, New York.

117. G., J. F. 1902. Habits of Lungoor Monkey. *Journ. Bomb. Nat. Hist. Soc.*, Vol. 14, pp. 149–151.

118. GANDER, FRANK F. 1929. Experiences with Wood Rats, *Neotoma fuscipes macrotis. Journ. Mamm.*, Baltimore, Vol. 10, pp. 52–58.

119. GARNER, R. L. 1892. *The Speech of Monkeys.* Heinemann. London.

120. ——— 1896. *Gorillas and Chimpanzees.* London.

121. ——— 1914. Gorillas in their own Jungle. *New York Zool. Soc. Bull.*, Vol. 17, pp. 1102–1104.

122. ——— 1918. Troops of Chimpanzees. *New York Zool. Soc. Bull.*, Vol 21, p. 1566.

123. GEAR, H. S. 1926. The Œstrous Cycle of the Baboon. *S. A. Journ. Sci.*, Capetown, Vol. 23, pp. 706–712.

124. GENTHER, IDA T. 1931. Irradiation of the Ovaries of Guinea-pigs and its effect on the Œstrous Cycle. *Amer. Journ. Anat.*, Philadelphia, Vol. 48, pp. 99–130.

125. GRAY, J. E. 1861. On the Habits of the Gorilla and other Tailless Long-Armed Apes. *Proc. Zool. Soc.*, London, pp. 212–213.

126. GREGG, F. M., and MCPHEETERS, C. A. 1913. Behavior of Raccoons to a temporal series of Stimuli. *Journ. Anim. Behav.*, Boston, Vol. 3, No. 3, pp. 241–259.

127. GREGG, F. M., JAMISON, E., WILKIE, R., and RADINSKY, T., 1929. Are Dogs, Cats and Raccoons color blind? *Journ. Comp. Psych.*, Baltimore, Vol. 9, pp. 379–395.

128. GRIFFITH, E., HAMILTON-SMITH, C., and PIDGEON, E. 1827. *The Class Mammalia arranged by the Baron Cuvier*, Vol. 1. Whittaker. London.

129. GRINNELL, J. 1922. A Geographical Study of the Kangaroo Rats of California. *Univ. Calif. Pub. Zool.*, Vol. 24, No. 1, pp. 1–124.

130. ——— 1929. Pronghorn Antelope. *Journ. Mamm.*, Baltimore, Vol. 10, pp. 135–141.

131. GUDGER, E. W. 1919. Monkeys Trained to Pick Coconuts. *Science*, New York, Vol. 49, pp. 146–147.

132. GYLDENSTOLPE, N. 1923. Among the Giant Volcanoes. *Cent. Mag.*, New York, Vol. 84, pp. 578–587.

133. H., C. 1880. Sketches of Natural History at Gibraltar. *The Field*, London, Vol. 56, p. 79.

134. HAAGNER, A. K. 1920. *South African Mammals*. Witherby. London.

135. HAGGERTY, M. E. 1909. Imitation in Monkeys. *Journ. Comp. Neur. & Psych.*, Philadelphia, Vol. 19, pp. 337–441.

136. HAMILTON, G. V. 1914. A Study of Sexual Tendencies in Monkeys and Baboons. *Journ. Anim. Behav.*, Boston, Vol. 4, pp. 295–318.

137. HAMMOND, J., and MARSHALL, F. H. A. 1925. *Reproduction in the Rabbit*. Oliver & Boyd. London.

138. ——— 1930. Œstrus and Pseudo-Pregnancy in the Ferret. *Proc. Roy. Soc.*, London, B, Vol. 105, pp. 607–630.

139. HARTMAN, C. G. 1927. Menstruation without Ovulation in *Macacus rhesus*. *Anat. Rec.*, Philadelphia, Vol. 35, p. 13 (Abstract).

140. ——— 1928. Menstruation in *Macacus rhesus* with Interval Endometrium. *Anat. Rec.*, Philadelphia, Vol. 38, p. 47 (Abstract).

141. ——— 1928. Description of Parturition in *Macacus rhesus*, together with Data on the Gestation Period and the Phenomena incident to Pregnancy and Labor. *Bull. Johns Hopkins Hospital*, Baltimore, Vol. 43, pp. 33–51.

142. ——— 1928. The Period of Gestation in the Monkey (*Macacus rhesus*): First Description of Parturition in Monkeys, Size and Behavior of the Young. *Journ. Mamm.*, Baltimore, Vol. 9, pp. 181–194.

143. ——— 1928. A readily detectable Sign of Ovulation in the Monkey. *Science*, New York, Vol. 68, pp. 452–453.

144. ——— 1929. Three Types of Uterine Bleeding in the Monkey and the Homology of Menstruation. *Anat. Rec.*, Philadelphia, Vol. 42, p. 61 (Abstract).

145. ——— 1929. Uterine Bleeding as an Early Sign of Pregnancy in the Monkey (*Macacus rhesus*), together with Observations on the Fertile Period of the Menstrual Cycle. *Bull. Johns Hopkins Hospital*, Baltimore, Vol. 44, pp. 155–164.

146. ——— 1929. The Homology of Menstruation. *Journ. Amer. Med. Assoc.*, Chicago, Vol. 92, pp. 1992–1995.

147. ——— 1929. A Breeding and a Non-Breeding Season in the Monkey, *Macacus rhesus*. *Anat. Rec.*, Philadelphia, Vol. 44, p. 226 (Abstract).

148. ——— 1929. The Fertile Period of the Menstrual Cycle in the Monkey. *Anat. Rec.*, Philadelphia, Vol. 44, p. 226 (Abstract).

149. HARTMAN, C. G. 1928. Gestation in a Monkey (*Macacus rhesus*) and Associated Phenomena. *Amer. Journ. Obst. & Gynecol.*, St. Louis, Vol. 15, pp. 534–540.

150. ——— 1930. Reproductive Phenomena in the Monkey, *Macacus rhesus*. *Amer. Journ. Obst. & Gynecol.*, St. Louis, Vol. 19, pp. 405–410.

151. ——— 1930. The Corpus Luteum and the Menstrual Cycle together with the Correlation between Menstruation and Implantation. *Amer. Journ. Obst. & Gynecol.*, St. Louis, Vol. 19, pp. 511–519.

152. ——— 1930. Anterior Lobe of the Pig and the Monkey Ovary. *Proc. Soc. Exp. Biol. & Med.*, New York, Vol. 27, pp. 338–340.

153. ——— 1931. The Breeding Season in Monkeys, with special reference to *Pithecus* (*Macacus*) *rhesus*. *Journ. Mamm.*, Baltimore, Vol. 12, pp. 129–142.

154. HARTMAN, C. G., SQUIER, R. R., and TINKLEPAUGH, O. L. 1930. The Fetal Heart Rate in the Monkey (*Macacus rhesus*). *Proc. Soc. Exp. Biol. & Med.*, New York, Vol. 28, pp. 285–288.

155. HARTMAN, C. G., FIROR, W. M., and GEILING, E. M. K. 1930. The Anterior Lobe and Menstruation. *Amer. Journ. Physiol.*, Baltimore, Vol. 95, pp. 662–669.

156. ——— 1930. Menstruation and the Anterior Pituitary. *Proc. Soc. Exp. Biol. & Med.*, Vol. 28, pp. 185–187.

157. HARTMANN, R. 1885. *Anthropoid Apes*. Kegan Paul, Trench. London.

158. HASTED, H. R. G. 1906. An Injured Monkey. *Journ. Bomb. Nat. Hist. Soc.*, Bombay, Vol. 17, p. 1017.

159. HEAPE, W. 1894. The Menstruation of *Semnopithecus entellus*. *Phil. Trans. Roy. Soc.*, London, B, Vol. 185, pp. 411–471.

160. ——— 1896. The Menstruation and Ovulation of *Macacus rhesus*. *Proc. Roy. Soc.*, London, Vol. 60, pp. 202–205.

161. ——— 1897. The Menstruation and Ovulation of *Macacus rhesus*, with Observations on the Changes undergone by the Discharged Follicle.—Part II. *Phil. Trans. Roy. Soc.*, London, B, Vol. 188, pp. 135–166.

162. ——— 1898. The Menstruation and Ovulation of Monkeys and the Human Female. *Trans. Obst. Soc.*, London, Vol. 40, pp. 161–174.

163. ——— 1899. Abortion, Barrenness, and Fertility in Sheep. *Journ. Roy. Agric. Soc.*, 3rd Series, London, Vol. 10, pp. 217–248.

164. ——— 1899. Note on the Fertility of Different Breeds of Sheep, with Remarks on the Prevalence of Abortion and Barrenness therein. *Proc. Roy. Soc.*, London, Vol. 65, pp. 99–111.

165. HEAPE, W. 1900. The "Sexual Season" of Mammals and the Relation of the "Pro-œstrum" to Menstruation. *Quart. Journ. Micros. Sci.*, London, Vol. 44, pp. 1–70.

166. HELLER, E. 1913. New Races of Ungulates and Primates from Equatorial Africa. *Smithson. Misc. Coll.*, Washington, D.C., Vol. 61, No. 17, pp. 1–12.

167. ——— 1913. New Races of Carnivores and Baboons from Equatorial Africa and Abyssinia. *Smithson. Misc. Coll.*, Washington, D.C., Vol. 61, No. 19, pp. 1–12.

168. HICKSON, S. J. 1889. *A Naturalist in North Celebes.* John Murray. London.

169. HILL, J. P., and O'DONOGHUE, C. H. 1913. The Reproductive Cycle in the Marsupial *Dasyurus viverinus*. *Quart. Journ. Micros. Sci.*, London, Vol. 59, pp. 133–174.

170. HILL, M., and PARKES, A. S. 1930. The Relation between the Anterior Pituitary Body and the Gonads. Part I—The Factors concerned in the Formation of the Corpus luteum. Part II—The Induction of Ovulation in the Anoestrous Ferret. *Proc. Roy. Soc.*, London, B, Vol. 107, pp. 30–49.

171. ——— 1931. Studies in Ovulation. IV. Induction of ovulation in the hypophysectomized rabbit by administration of anterior lobe extract. *Journ. Physiol.*, London, Vol. 71, No. 1, pp. 36–39.

172. ——— 1931. Studies in Ovulation. V. The Actions of the ovulation-producing substance of urine of pregnancy on the hypophysectomized rabbit. *Journ. Physiol.*, London, Vol. 71, pp. 40–46.

173. HINGSTON, R. W. G. 1920. *A Naturalist in Himalaya.* Witherby. London.

174. HISAW, F. L., FEVOLD, H. L., and MEYER, R. K. 1930. The Function of Follicular and Corpus Luteum Hormones in the production of a Premenstrual Endometrium in the Uterus of Castrate Monkeys (*Macacus rhesus*). *Anat. Rec.*, Philadelphia, Vol. 47, p. 300 (Abstract).

175. HISAW, F. L., and LEONARD, S. L. 1930. Relation of the Follicular and Corpus Luteum Hormones in the Production of Progestational Proliferation of the Rabbit's Uterus. *Amer. Journ. Physiol.*, Baltimore, Vol. 92, pp. 574–582.

176. HITZHEIMER, M., and HECK, L. 1925. *Die Säugetiere von Alfred Brehm.* Vierter Band. Leipzig.

177. HOBHOUSE, L. T. 1901. *Mind in Evolution.* Macmillan. London.

178. HOFSCHLÄGER, R. 1925. Geschlecht und Gesellschaft in der Zeit der Menschwerdung. *Geschlecht und Gesellschaft*, Dresden, Bd. 13, pp. 1–34.

179. HOGBEN, L. 1930. *The Nature of Living Matter.* Kegan Paul, Trench, Trubner & Co. London.

180. HOGBEN, L., CHARLES, E., and SLOME, D. 1931. Studies on the Pituitary. VIII. Relation of the Pituitary to the Ovaries and Blood Calcium. *Journ. Exp. Biol.*, Lond., Vol. 8, pp. 345–354.

181. HOLLISTER, N. 1916. A Systematic Account of the Prairie-Dogs. *N. American Fauna*, Washington, No. 40, pp. 1–36.

182. HOLT, F. B. 1931. *Animal Drive and the Learning Process.* Vol. 1. Williams & Norgate. London. Pp. 307.

183. HORNADAY, W. T. 1879. On the Species of the Bornean Orangs, with Notes on their Habits. *Proc. Amer. Assoc. Advanc. Sci.*, Salem, 20th Meeting, pp. 438–455.

184. ——— 1885. *Two Years in the Jungle; the Experiences of a Hunter and Naturalist in India, Ceylon, the Malay Peninsula, and Borneo.* London.

185. ——— 1915. Gorillas Past and Present. *New York Zool. Soc. Bull.*, Vol. 18, pp. 1181–1185.

186. ——— 1922. *The Minds and Manners of Wild Animals.* Scribner. New York.

186A. HOSE, C. 1893. *Descriptive account of the Mammals of Borneo.* London. Pp. 78.

187. HOSKINS, R. G. 1925. Studies on Vigor. II. The Effect of Castration on Voluntary Activity. *Amer. Journ. Physiol.*, Baltimore, Vol. 72, pp. 324–330.

188. HOWARD, H. E. 1929. *An Introduction to the Study of Bird Behaviour.* Camb. Univ. Press.

188A. HOWELL, A. B. 1919. Notes on the Californian Mastiff-bat. *Journ. Mamm.*, Baltimore, Vol. 1, pp. 111–117.

189. ——— 1927. Revision of the American Lemming Mice. *N. American Fauna*, Washington, No. 50, pp. 1–38.

190. HUGHES, T. H. 1884. An Incident in the Habits of the *Semnopithecus entellus*, the Common Hanuman Monkey. *Proc. Asiatic Soc. Bengal*, Calcutta, pp. 147–150.

190A. HUNTER, W. S. 1913. The Question of Form Perception. *Journ. Anim. Behav.*, Boston, Vol. 3, pp. 329–333.

191. ——— 1914. The Auditory Sensitivity of the White Rat. *Journ. Anim. Behav.*, Boston, Vol. 4, pp. 215–222.

192. HUTTON, T. 1867. On the Geographical Range of *Semnopithecus entellus.* *Proc. Zool. Soc.*, London, pp. 944–952.

193. HUXLEY, T. H. 1863. *Man's Place in Nature.* Everyman's Library Edition: Dent. London. 1921.

194. ISHII, O. 1920. Observations on the Sexual Cycle of the Guinea-pig. *Biol. Bull.*, Wood's Hole, Mass., Vol. 38, pp. 237–250.

195. JACOBSEN, C. F. 1931. A Study of Cerebral Function in Learning. The Frontal Lobes. *Journ. Comp. Neurol.*, Philadelphia, Vol. 52, No. 2, pp. 271–340.

196. JENKS, A. E. 1911. Bulu Knowledge of the Gorilla and Chimpanzee. *Amer. Anth.*, Lancaster, Pa., N.S., Vol. 13, pp. 56–58.

197. JENNISON, G. 1915. A Nest-Making Chimpanzee. *Proc. Zool. Soc.*, London, pp. 535–536.

198. JERDON, T. C. 1867. *The Mammals of India.* Thomason College Press. Roorkee.

199. JOACHIMOVITS, R. 1928. Studien zu Menstruation, Ovulation, Aufbau und Pathologie des weiblichen Genitales bei Mensch und Affe (*Pithecus fascicularis mordax*). *Biologia Generalis*, Vienna, Bd. 4, pp. 447–540.

200. JOHNSON, E. L. 1924. Relation of Sheep to Climate. *Journ. Agric. Res.*, Washington, Vol. 29, pp. 491–500.

201. JOHNSON, H. M. 1914. Hunter on the question of form-perception in animals. *Journ. Anim. Behav.*, Boston, Vol. 4, No. 2, pp. 134–135.

202. ——— 1914. Visual pattern-discrimination in the vertebrates. I. Problems and Methods. *Journ. Anim. Behav.*, Boston, Vol. 4, No. 5, pp. 319–339.

203. ——— 1914. Visual Pattern-discrimination in the Vertebrates. II. Comparative Visual Acuity in the Dog, the Monkey and the Chick. *Journ. Anim. Behav.*, Boston, Vol. 4, No. 5, pp. 340–361.

204. ——— 1916. Visual Pattern-discrimination in the Vertebrates. III. Effective Differences in Width of Visible Striæ for the Monkey and Chick. *Journ. Anim. Behav.*, Boston, Vol. 6, pp. 169–188.

205. ——— 1916. IV. Effective Difference in Direction of Visible Striæ for the Monkey and Chick. Ibid, pp. 189–204.

206. ——— 1916. V. A Demonstration of the Dog's Deficiency in Detail-vision. Ibid, pp. 205–221.

207. JOHNSTON, H. H. 1885. General Observations on the Fauna of Kilima-njaro. *Proc. Zool. Soc.*, London, pp. 215–218.

208. ——— 1886. *The Kilima-njaro Expedition.* London.

209. KEARTON, C. 1929. *In the Land of the Lion.* Arrowsmith. London.

210. KELAART, F. 1852. *Prodromus Faunae Zeylanicae: Being contributions to the Zoology of Ceylon.* Colombo and London.

211. KEMPF, EDWARD J. 1917. The Social and Sexual Behavior of Infra-human Primates, with some Comparable Facts in Human Behavior. *Psychoanalytic. Rev.*, New York, Vol. 4, pp. 127–154.

212. KENDREW, W. G. 1927. *The Climates of the Continents.* Oxford.

213. KINDER, E. F. 1927. A Study of Nest-building Activity of the Albino Rat. *Journ. Exper. Zool.*, Philadelphia, Vol. 47, pp. 117–161.

214. KIRK, J. 1884. On the Occurrence of *Colobus kirkii*. *Ann. Mag. Nat. Hist.*, London, (5) Vol. 13, p. 307.

215. KIRKHAM, WM. B., and BURR, H. S. 1913. The Breeding Habits, Maturation of Eggs and Ovulation of the Albino Rat. *Amer. Journ. Anat.*, Philadelphia, Vol. 15, pp. 291–317.

216. KLOSS, C. B. 1908. The White-Handed Gibbon. *Journ. Straits Br. R. Asiatic Soc.*, Singapore, Vol. 50, pp. 79–80.

217. KÖHLER, W. 1927. *The Mentality of Apes*. Translated from the Second Revised Edition by Ella Winter, B.Sc. Kegan Paul, Trench, Trubner & Co., Ltd. London.

218. ——— 1930. *Gestalt Psychology*. Bell. London.

219. KOHTS, N. 1923. *Untersuchungen über die Erkenntnisfähigkeiten des Schimpansen*. Moscow.

220. ——— 1928. *Adaptive Motor Habits of the Macacus rhesus under Experimental Conditions*. A contribution to the problem of "Labour Processes" of Monkeys. Moscow.

221. KOPPENFELS, HUGO VON. 1877. Meine Jagden Auf Gorillas. *Gartenlaube*, Leipzig, pp. 416–420.

222. KROEBER, A. L. 1928. Sub-Human Culture Beginnings. *Quart. Rev. Biol.*, Baltimore, Vol. 3, pp. 325–342.

223. KROPOTKIN, P. A. 1919. *Mutual Aid*. Heinemann. London.

224. LANGLEY, J. N. 1890. The Innervation of the Pelvic Viscera. *Journ. Physiol.*, London, Vol. 12, No. 6, pp. xxiii-xxvi.

225. LANGLEY, J. N., and SHERRINGTON, C. S. 1891. On Pilo-motor Nerves. *Journ. Physiol.*, London, Vol. 12, pp. 278–291.

226. LA RUE, C. D. 1919. Monkeys as Coconut Pickers. *Science*, New York, Vol. 50, p. 187.

227. LASHLEY, K. S. 1915. Notes on the Nesting Activities of the Noddy and Sooty Terns. *Papers from the Dept. of Marine Biology of the Carnegie Inst. of Washington*, Vol. 7, pp. 61–84.

228. ——— 1917. Modifiability of the Preferential Use of the Hands in the Rhesus Monkey. *Journ. Anim. Behav.*, Boston, Vol. 7, pp. 178–186.

229. ——— 1929. *Brain Mechanisms and Intelligence*. Univ. of Chicago Press. Chicago.

230. LASHLEY, K. S., and WATSON, J. B. 1913. Notes on the Development of a Young Monkey. *Journ. Anim. Behav.*, Boston, Vol. 3, pp. 114–139.

231. LENZ, H. 1891. Einiges über das Freileben der Nasenaffen *Nasalis larvatus*. *Zool. Gart.*, Frankfürt, Vol. 32, pp. 216–218.

232. LINDSAY, W. L. 1879. *Mind in the Lower Animals*, Vol. 1. Kegan Paul. London.

233. LOEB, J. 1906. *The Dynamics of Living Matter*. Columbia Univ. Press. New York.

234. LONG, J. A., and EVANS, H. M. 1922. The Œstrous Cycle in the Rat, and its Associated Phenomena. *Mem. Univ. Calif.*, Berkeley, Vol. 6.

235. LÖNNBERG, E. 1908. On a New Guereza (*Colobus angolensis Sandbergi*) and remarks on other black and white Guerezas. *Ark. Zool.*, Stockholm, Vol. 4, No. 15, pp. 1–12.

236. LOUTTIT, C. M. 1927. Reproductive Behavior of the Guinea-Pig. I. Normal Mating Behavior. *Journ. Comp. Psych.*, Baltimore, Vol. 7, pp. 247–263.

237. ——— 1929. Reproductive Behavior of the Guinea-Pig. II. The Ontogenesis of the Reproductive Behavior Pattern. *Journ. Comp. Psych.*, Baltimore, Vol. 9, pp. 293–304.

238. ——— 1929. Reproductive Behavior of the Guinea-Pig. III. Modification of the Behavior Pattern. *Journ. Comp. Psych.*, Baltimore, Vol. 9, pp. 305–316.

239. LOVERIDGE, A. 1921. Notes on East African Mammalia (other than Horned Ungulates) collected or kept in Captivity. 1915–1919. *Journ. E. Afr. & Uganda N.H. Soc.*, London, No. 16, pp. 38–42; No. 17, pp. 39–69.

239A. ——— 1923. Notes on East African Mammals. *Proc. Zool. Soc.*, London, pp. 685–739.

240. LUCAS, N. S., HUME, M., and SMITH, H. H. 1927. On the Breeding of the Common Marmoset (*Hapale jacchus* Linn.) in Captivity when irradiated with Ultra-violet Rays. *Proc. Zool. Soc.*, London, pp. 447–451.

241. LYDEKKER, R. 1895. *Handbook to the British Mammalia*. W. H. Allen & Co. London.

242. ——— 1898. *The Deer of All Lands*. Rowland Ward. London.

243. ——— 1912. *The Sheep and its Cousins*. Allen. London.

244. MADDUX, W. P. 1930. Experimentally induced Intermenstrual Bleeding in Ovariectomized Monkeys. *Proc. Soc. Exp. Biol. & Med.*, New York, Vol. 27, pp. 873–874.

245. MALINOWSKI, B. 1927. *Sex and Repression in Savage Society*. Kegan Paul, Trench, Trubner & Co., Ltd. London.

246. MARAIS, E. N. 1926. Baboons, Hypnosis, and Insanity. *Psyche*, London, No. 26, pp. 104–110.

247. MARSHALL, F. H. A. 1903. The Œstrous Cycle and the Formation of the Corpus Luteum in the Sheep. *Phil. Trans. Roy. Soc.*, London, B, Vol. 196, pp. 47-98.

248. ——— 1905. Fertility in Scottish Sheep. *Proc. Roy. Soc.*, London, B, Vol. 77, pp. 58–62.

249. ——— 1908. The Effect of Environment and Nutrition on Fertility. *Sci. Prog.*, London, Vol. 2, pp. 369–377.

250. MARSHALL, F. H. A. 1922. *The Physiology of Reproduction.* Longmans, Green & Co. London. 2nd edition.

251. ——— 1927. On the Pro-œstrum and Pseudo-Pregnancy. *Quart. Journ. Exp. Physiol.*, London, Vol. 17, pp. 205–210.

252. MARSHALL, F. H. A., and JOLLY, W. 1905. Contributions to the Physiology of Mammalian Reproduction. Part I. The Œstrous Cycle in the Dog. *Phil. Trans. Roy. Soc.*, London, B, Vol. 198, pp. 99–122.

253. MARSHALL, F. H. A., and HALNAN, E. T. 1917. On the Post-œstrous Changes occurring in the Generative Organs and Mammary Glands of the Non-Pregnant Dog. *Proc. Roy. Soc.*, London, B, Vol. 89, pp. 546–559.

254. MAXWELL, MARIUS. 1928. The Home of the Eastern Gorilla. *Journ. Bomb. Nat. Hist. Soc.*, Vol. 32, pp. 436–449.

255. MCMASTER, A. C. 1870. *Notes on Jerdon's Mammals of India.* Higginbotham. Madras.

256. MERRIAM, C. H. 1889. North American Pocket Mice. *N. American Fauna*, Washington, No. 1, pp. 36.

257. MIDDLETON, A. D. 1930. The Ecology of the American Gray Squirrel (*Sciurus carolinensis* (*Gruelin*)) in the British Isles. *Proc. Zool. Soc.*, London, pp. 809–843.

258. MILLER, GERRIT S. 1928. Some Elements of Sexual Behavior in Primates, and their Possible Influence on the Beginnings of Human Social Development. *Journ. Mammalogy*, Baltimore, Vol. 9, pp. 273–293.

259. MILLER, NEWTON. 1911. Reproduction in the Brown Rat. *Amer. Natural.*, New York, Vol. 45, pp. 623–635.

260. MONTANÉ, L. 1916. A Cuban Chimpanzee. C. S. Rossy (translator). *Journ. Anim. Behav.*, Boston, Vol. 6, pp. 330–333.

261. ——— 1928. Histoire d'une famille de Chimpanzé. *Bull. Mem. Soc. Anth.*, Paris, 7e. ser. Tom. 9, pp. 14–35.

262. MORGAN, C. LLOYD. 1890–91. *Animal Life and Intelligence.* Arnold. London. Pp. 1–512.

263. ——— 1894. *An Introduction to Comparative Psychology.* Scott. London. Pp. 382.

264. ——— 1900. *Animal Behaviour.* Arnold. London.

265. MORGULIS, SERGIUS. 1914. The Auditory Reactions of the Dog studied by the Pawlow Method. *Journ. Anim. Behav.*, Boston, Vol. 4, No. 2, pp. 142–145.

266. MORLEY, R. 1899. The Extermination of Monkeys (*Colobus vellerosus*) on the Gold Coast. *Nature Notes*, London, Vol. 10, pp. 113–114.

267. MOSS, F. A. 1924. Study of Animal Drives. *Journ. Exp. Psych.*, Princeton, Vol. 7, pp. 165–185.

268. MUIR, G. B. F. 1915. Monkeys (*Macacus rhesus*) swimming. *Journ. Bomb. Nat. Hist. Soc.*, Vol. 24, p. 353.

269. MUNN, N. L. 1930. Visual Pattern Discrimination in the Rat. *Journ. Comp. Psych.*, Baltimore, 10, pp. 145–166.

270. MURIE, J. 1872. Observations on the Macaques. III. The Formosan or Round-Faced Monkey. *Proc. Zool. Soc.*, London, pp. 771–780.

271. NELSON, E. W. 1925. Status of the Prong-horned Antelope, 1922–1924. *U.S. Dept. Agric. Bulletin*, Washington, No. 1346, pp. 1–64.

272. NELSON, W. O. 1929. Œstrus during Pregnancy. *Science*, New York, Vol. 70, pp. 453–454.

273. NELSON, W. O., and PFIFFNER, J. J. 1930. An Experimental Study of the Factors concerned in Mammary Growth and in Milk Secretion. *Proc. Soc. Exp. Biol. & Med.*, New York, Vol. 28, pp. 1–2.

274. NEUMANN, O. 1896. Über die geographische Verbreitung der Colobusaffen in Ost-Africa und deren Lebensweise. *Sitz. Ges. Naturf. Freunde*, Berlin, pp. 151–156.

275. NICHOLS, J. E. 1927. Meteorological Factors Affecting the Fertility of Sheep. *Zeitschrift fur induk. Abstam. und Vehers.*, Berlin, Band 43, pp. 313–329.

276. ——— 1929. Some Observations on the Problem of Fertility and Fecundity in Sheep. *Zeitschrift für Tier. und Züch.*, Berlin, Band 10, pp. 225–234.

277. NICHOLLS, EDITH E. 1922. A Study of the Spontaneous Activity of the Guinea-pig. *Journ. Comp. Psychol.*, Baltimore, Vol. 2, pp. 303–330.

278. NORTHCOTE, G. A. S. 1921. Baboons attacking Children. *Journ. E. Afr. & Uganda N. H. Soc.*, London, No. 16, pp. 60–61.

279. PARKES, A. S. 1926. The Mammalian Sex Ratio. *Biol. Rev.*, Cambridge, Vol. 2, pp. 1–51.

280. ——— 1926. Observations on the Œstrous Cycle of the Albino Mouse. *Proc. Roy. Soc.*, London, B, Vol. 100, pp. 151–170.

281. ——— 1929. *The Internal Secretions of the Ovary*. Longmans, Green & Co. London.

282. PARKES, A. S., and BRAMBELL, F. W. R. 1928. The Causation of the Anœstrous Period. *Journ. Physiol.*, London, Vol. 64, pp. 388–392.

283. PARKES, A. S., and ZUCKERMAN, S. 1931. The Menstrual Cycle of the Primates. Part II. Some Effects of Œstrin on Baboons and Macaques. *Journ. Anat.*, Cambridge, Vol. 65, pp. 272–276.

284. PARR, A. E. 1927. A Contribution to the Theoretical Analysis of the Schooling Behavior of Fish. *Occasional Papers of the Bingham Oceanographic Collection*. New York. No. 1. Pp. 1–32.

285. Pavlov, I. P. 1927. *Conditioned Reflexes*. Translated and edited by G. V. Anrep. Oxford Univ. Press.

286. Pocock, R. I. 1905. Observations upon a Female Specimen of the Hainan Gibbon (*Hylobates hainanus*) now living in the Society's Gardens. *Proc. Zool. Soc.*, London, Vol. 2, pp. 169–180.

287. ——— 1906. Notes upon Menstruation, Gestation, and Parturition of some Monkeys that have lived in the Society's Gardens. *Proc. Zool. Soc.*, London, Vol. 2, pp. 558–570.

288. ——— 1925. The External Characters of the Catarrhine Monkeys and Apes. *Proc. Zool. Soc.*, London, pp. 1479–1579.

289. Rabaud, E. 1921. L'instinct Maternel chez les Mammifères. *Bull. Soc. Zool.*, Paris, Tome 46, pp. 73–81.

290. Reade, W. Winwood. 1863. *Savage Africa*. Smith Elder. London.

291. Reading, J. H. 1884. The Habits of the Gorilla. *Amer. Nat.*, New York, Vol. 18, p. 1227.

292. Reichenow, E. 1920. Biologische Beobachtungen an Gorilla und Schimpanse. *Sitz. Ges. Naturforsch. Freunde*, Berlin, pp. 1–40.

293. Rengger, J. R. 1830. *Naturgeschichte der Säugethiere von Paraguay*. Basel.

294. Rèvèsz, G. 1925. Experimental Study in Abstraction in Monkeys. *Journ. Comp. Psychol.*, Baltimore, Vol. 5, pp. 293–341.

295. Ridley, H. N. 1895. The Mammals of the Malay Peninsula. *Nat. Sci.*, London, Vol. 6, pp. 23–29, 89–96, 161–166.

296. Robertson, D. C. 1929. Effects induced in Ovariectomized Monkeys by Injections of Extracts of Ovaries and Implants of Corpora Lutea. *Anat. Rec.*, Philadelphia, Vol. 42, p. 61 (Abstract).

297. Robertson, D. C., Maddux, W. P., and Allen, E. 1930. Ovarian Hormone Effects in Ovariectomised Monkeys. *Endocrinology*, Glendale, Cal., Vol. 14, pp. 77–88.

298. Romanes, G. J. 1882. *Animal Intelligence*. Kegan Paul, Trench & Co. London.

299. Roosevelt, T. 1914. *Through the Brazilian Wilderness*. Scribner's. New York.

300. Royer, C. 1887. La Domestication des Singes. *Rev. d'Anth.*, Paris, Tome 2, pp. 170–181.

301. Rowley, J. 1929. Life-History of the Sea-Lions on the California Coast. *Journ. Mamm.*, Baltimore, Vol. 10, pp. 1–36.

302. Russell, B. 1927. *An Outline of Philosophy*. Allen & Unwin. London.

303. SÀNYÀL, BABU RAM BRAMHA. 1893. Hybridization between *Semnopithecus phayrei* and *S. cristatus*. *Proc. Zool. Soc.*, London, p. 615.

304. SAVAGE, T. S., and WYMAN, J. 1844. Observations on the External Characters and Habits of the *Troglodytes niger, Geof.*, and on its Organization. *Bost. Journ. of Nat. Hist.*, Vol. 4, pp. 362–386.

305. SCHEFFER, T. H. 1924. Notes on the Breeding of *Peromyscus*. *Journ. Mamm.*, Baltimore, Vol. 5, pp. 258–260.

306. SCHULTZ, A. H. 1921. The Occurrence of a Sternal Gland in the Orang Utan. *Journ. Mamm.*, Baltimore, Vol. 2, pp. 194–196.

307. SCHUSTER, L. 1929. Ein Beitrag zur Frage der Brunst- und Setzzeiten der Säugetiere in den Tropen. *Zool. Garten*, Leipzig, Vol. 2, pp. 114–117.

308. SCHWARZ, E. 1927. Un Gorille nouveau de la forêt de l'Ituri. *Rev. Zool. Africaine*, Bruxelles, Vol. 14, fasc. 3, pp. 333–336.

309. SCHWEINFURTH, G. 1873. *The Heart of Africa*. Vol. 1. Sampson Low, Marston, Low & Searle. London.

310. SCLATER, P. L. 1864. Notes on the Quadrumana living in the Society's Menagerie. *Proc. Zool. Soc.*, London, pp. 709–712.

311. ——— 1900. On the *Macacus inuus* of Gibraltar. *Proc. Zool. Soc.*, London, pp. 773–774.

312. SCLATER, W. L. 1900. *The Mammals of South Africa*. Vols. 1 and 2. Porter. London.

313. SCLATER, W. L., and SCLATER, P. L. 1899. *The Geography of Mammals*. Kegan Paul. London.

314. SCOTT-ELLIOT, G. F. 1895. Expedition to Central Africa. Notes on Animals collected round Mount Ruwenzori. *Proc. Zool. Soc.*, London, pp. 339–343.

315. SETON, E. T. 1910. *Life-Histories of Northern Animals*. Vols. 1 and 2. Constable. London.

316. SHARPE, NEVILLE A. DYCE. 1927. Notes on the Gorilla. *Proc. Zool. Soc.*, London, pp. 1006–1009.

317. SHAW, WILFRED. 1927. Ovulation in the Human Ovary: its Mechanism and Anomalies. *Journ. Obstet. & Gynæcol. of Brit. Emp.*, Manchester, Vol. 34, pp. 469–480.

318. ——— 1928. Notes on the Comparative Physiology of the Menstrual Cycle. *Saint Bartholomew's Hospital Reports*, London, Vol. 62, pp. 193–203.

319. SHELFORD, R. W. C. 1916. *A Naturalist in Borneo*. London.

320. SHEPHERD, W. T. 1914. On Sound Discrimination by Cats. *Journ. Anim. Behav.*, Boston, Vol. 4, pp. 70–75.

321. ——— 1915. Some Observations on the Intelligence of the Chimpanzee. *Journ. Anim. Behav.*, Boston, Vol. 5, pp. 391–396.

322. SHEPHERD, W. T. 1915. Tests on Adaptive Intelligence in Dogs and Cats as compared with Adaptive Intelligence in *Rhesus* Monkeys. *Amer. Journ. Psych.*, Worcester, Mass., Vol. 26, pp. 211–216.

323. SHERRINGTON, C. S. 1892. Notes on the Arrangement of some Motor Fibres in the Lumbo-sacral Plexus. *Journ. Physiol.*, London, Vol. 13, pp. 621–772.

324. ——— 1892. Experiments in Examination of the Peripheral Distribution of the Fibres of the Posterior Roots of some Spinal Nerves. *Proc. Roy. Soc.*, London, Vol. 52, pp. 333–337.

325. SIGEL, W. L. 1883. Beobachtungen aus dem Tierleben in Zoologischen Garten zu Hamburg. *Zool. Gart.*, Frankfürt, Bd. 24, pp. 235–237.

326. SIMPSON, G. G. 1931. A New Classification of Mammals. *Bull. Amer. Mus. of Nat. Hist.*, New York, Vol. 59, Art. 5, pp. 259–293.

327. SLONAKER, JAMES ROLLIN. 1924. The Effect of Pubescence, Œstruation and Menopause on the Voluntary Activity of the Albino Rat. *Amer. Journ. Physiol.*, Baltimore, Vol. 68, pp. 294–315.

328. ——— 1925. The Effects of Copulation, Pregnancy, Pseudo-pregnancy and Lactation on the Voluntary Activity and Food Consumption of the Albino Rat. *Amer. Journ. Physiol.*, Baltimore, Vol. 71, pp. 362–394.

329. SMITH, E. M. 1923. *The Investigation of Mind in Animals.* University Press. Cambridge. Pp. 195.

330. SMITH, P. E., and ENGLE, E. T. 1927. Experimental Evidence Regarding the Rôle of the Anterior Pituitary in the Development and Regulation of the Genital System. *Ame Journ. Anat.*, Philadelphia, Vol. 40, pp. 159–218.

331. SOKOLOWSKY, ALEXANDER. 1923. The Sexual Life of the Anthropoid Apes. *Urologic and Cutaneous Review*, St. Louis, Vol. 27, pp. 612–615.

332. SPENCER, H. 1876. *Principles of Sociology.* Williams & Norgate. London.

333. SPIEGEL, A. 1929. Biologische Beobachtungen an Javamakaken, *Macacus irus* F. Cuv. (*cynomolgus* L.). *Zool. Anz.*, Leipzig, Bd. 81, pp. 45–65.

334. ——— 1930. Beobachtungen über den Sexualzyklus, die Gravidität und die Geburt bei Javamakaken (*Macaca irus mordax* Thomas & Wroughton (*cynomolgus* L.)). *Arch. Gynäk.*, Berlin, Bd. 142, pp. 561–591.

335. ——— 1931. Untersuchungen über die Fortpflanzung bei Javamakaken. *Zentralblatt für Gynäkologie*, Leipzig, Bd. 55, pp. 1762–1767.

336. STERNDALE, R. A. 1884. *Natural History of the Mammalia of India and Ceylon.* Thacker Spink & Co. Calcutta.

337. STEVENSON-HAMILTON, J. 1912. *Animal Life in Africa.* William Heinemann. London.

338. STONE, CALVIN P. 1922. The Congenital Sexual Behavior of the Young Male Albino Rat. *Journ. Comp. Psych.*, Baltimore, Vol. 2, pp. 95–153.

339. ——— 1924. The Awakening of Copulatory Ability in the Male Albino Rat. *Amer. Journ. Physiol.*, Baltimore, Vol. 68, pp. 407–423.

340. ——— 1924. A Note on "Feminine" Behavior in Adult Male Rats. *Amer. Journ. Physiol.*, Baltimore, Vol. 68, pp. 39–41.

341. ——— 1925. Preliminary Note on the Maternal Behavior of Rats living in Parabiosis. *Endocrinology*, Glendale, Cal., Vol. 9, pp. 505–512.

342. ——— 1925. Delay in the Awakening of Copulatory Ability in the Male Albino Rat incurred by Defective Diets. II. Qualitative Deficiency. *Journ. Comp. Psych.*, Baltimore, Vol. 5, pp. 177–203.

343. ——— 1925. The Effects of Cerebral Destruction on the Sexual Behavior of Rabbits. I. The Olfactory Bulbs. *Amer. Journ. Physiol.*, Baltimore, Vol. 71, pp. 430–435.

344. ——— II. The Frontal and Parietal Regions. *Amer. Journ. Physiol.*, Baltimore, Vol. 72, pp. 372–385.

345. ——— 1926. The Initial Copulatory Response of Female Rats reared in Isolation from the age of Twenty days to the age of Puberty. *Journ. Comp. Psychol.*, Baltimore, Vol. 6, pp. 73–84.

346. ——— 1926. The Effects of Cerebral Destruction on the Sexual Behavior of Male Rabbits. III. The Frontal, Parietal and Occipital Regions. *Journ. Comp. Psych.*, Baltimore, Vol. 6, pp. 435–448.

347. ——— 1927. The Retention of Copulatory Ability in Male Rats following Castration. *Journ. Comp. Psych.*, Baltimore, Vol. 7, pp. 369–387.

348. STRUTHERS, P. H. 1928. Breeding-Habits of the Canadian Porcupine (*Erethizon dorsatum*). *Journ. Mamm.*, Baltimore, Vol. 19, pp. 300–308.

349. STURMAN-HULBE, MARY, and STONE, CALVIN P. 1929. Maternal Behavior in the Albino Rat. *Journ. Comp. Psych.*, Baltimore, Vol. 9, pp. 203–238.

350. SWINHOE, R. 1870. On the Mammals of Hainan. *Proc. Zool. Soc.*, London, pp. 224–239.

351. TENNENT, J. E. 1861. *Natural History of Ceylon.* Longman, Green, Longman & Roberts. London.

352. THOMAS, O., and WROUGHTON, R. C. 1910. Ruwenzori Expedition Reports. No. 17, Mammalia. *Trans. Zool. Soc.*, London, Vol. 19, pp. 481–518.

353. THOMSON, G. M. 1922. *The Naturalization of Animals and Plants in New Zealand.* Cambridge Univ. Press.

354. THORNDIKE, E. L. 1911. *Animal Intelligence.* Macmillan. New York.

355. TICKELL, S. R. 1864. Note on the Gibbon (*Hylobates lar*) of Tenasserim. *Journ. Asiat. Soc. Bengal,* Calcutta, Vol. 33, pp. 196–199.

356. TINKLEPAUGH, OTTO LEIF. 1928. An Experimental Study of Representative Factors in Monkeys. *Journ. Comp. Psych.,* Baltimore, Vol. 8, pp. 197–236.

357. ——— 1928. The Self Mutilation of a Male *Macacus rhesus* Monkey. *Journ. Mamm.,* Baltimore, Vol. 9, pp. 293–300.

358. ——— 1930. Occurrence of Vaginal Plug in a Chimpanzee. *Anat. Rec.,* Philadelphia, Vol. 46, pp. 329–332.

359. ——— and HARTMAN, C. G. 1930. Behavioral Aspects of Parturition in the Monkey (*Macacus rhesus*). *Journ. Comp. Psych.,* Baltimore, Vol. 11, pp. 63–98.

360. ——— and VAN CAMPENHOUT, E. 1931. The Vaginal Cell Content of the Mature and Immature Chimpanzee. *Anat. Rec.,* Philadelphia, Vol. 48, pp. 309–322.

361. TOLMAN, E. C. 1928. Habit Formation and Higher Mental Processes in Animals. *Psych. Bull.,* Albany, Vol. 25, pp. 24–53.

362. TSAI, CHIAO. 1925. The Relative Strength of Sex and Hunger Motives in the Albino Rat. *Journ. Comp. Psych.,* Baltimore, Vol. 5, pp. 407–415.

363. TUR, JAN. 1909. Observations sur la perversion de l'instinct maternel. *Bull. Sci. France-Belgique,* Paris, Tome 43, pp. 477–480.

364. VALENTINE, WILLARD L. 1928. Visual Perception in the White Rat. *Journ. Comp. Psych.,* Baltimore, Vol. 8, pp. 369–375.

365. VAN HERWERDEN, M. 1905. *Bijdrage tot de Kennis van Menstrueelen Cyclus en Puerperium.* Brill. Leiden.

366. ——— 1925. Some Remarks on the Polyœstrus of Primates. *Anat. Rec.,* Philadelphia, Vol. 30, pp. 221–223.

367. WALLACE, A. R. 1890. *The Malay Archipelago.* 10th Edition. MacMillan. London.

368. WALSH, W. 1914. Commensualism between Monkeys, Tsaing and Deer. *Journ. Bomb. Nat. Hist. Soc.,* Vol. 23, p. 35.

369. WARDEN, C. J. 1928. *An Outline of Comparative Psychology.* Kegan Paul, Trench, Trubner & Co. London. Pp. 1–147.

370. ——— and WARNER, L. H. 1928. The Sensory Capacities and Intelligence of Dogs, with a report on the Ability

of the Noted Dog "Fellow" to Respond to Verbal Stimuli *Quart. Rev. Biol.*, Baltimore, Vol. 3, pp. 1–28.

371. WARNER, L. H. 1928. A Study of Hunger Behavior in the White Rat by means of the Obstruction Method. A Comparison of Sex and Hunger Behavior. *Journ. Comp. Psych.*, Baltimore, Vol. 8, pp. 273–299.

372. WASHBURN, M. F. 1908. *The Animal Mind.* Macmillan. New York. Pp. 333.

373. WATSON, J. B. 1908. Imitation in Monkeys. *Psych. Bull.*, Baltimore, Vol. 5, pp. 169–178.

374. ——— 1909. Some Experiments bearing upon Color-vision in Monkeys. *Journ. Comp. Neurol. & Psychol.*, Philadelphia, Pa., Vol. 19, pp. 1–28.

375. ——— 1914. *Behavior, an Introduction to Comparative Psychology.* Holt. New York. Pp. 439.

376. ——— 1931. *Behaviorism.* Norton. New York. 2nd ed. Pp. 308.

376a. WATT, H. J. 1925. *The Sensory Basis and Structure of Knowledge.* Methuen. London.

377. WESTERMARCK, E. 1921. *The History of Human Marriage.* Macmillan. London. 5th edition. Vol. 1.

378. WILLIAMS, J. A. 1926. Experiments with Form Perception and Learning in Dogs. *Comp. Psych. Monog.*, Baltimore, Vol. 4, pp. 1–70.

379. WINWOOD READE, W. 1868. The Habits of the Gorilla. *Amer. Nat.*, New York, Vol. 1, pp. 177–180.

380. WISLOCKI, G. B. 1930. On a Series of Placental Stages of a Platyrrhine Monkey (*Ateles Geoffroyi*) with some remarks upon age, sex, and breeding period in Platyrrhines. *Contrib. to Embryol.*, Carnegie Institute of Washington, Vol. 22, No. 133, pp. 172–192.

381. ——— 1930. A Study of Scent Glands in the Marmosets, especially *Oedipomidas geoffroyi.* *Journ. Mamm.*, Baltimore, Vol. 11, pp. 475–481.

382. ——— and HARTMAN, C. 1929. On the Placentation of a Macaque (*Macacus rhesus*), with Observations on the Origin of the Blood constituting the Placental Sign. *Bull. Johns Hopkins Hospital*, Baltimore, Vol. 44, pp. 165–185.

383. ——— and SCHULTZ, A. H. 1925. On the Nature of Modifications of the Skin in the Sternal Region of Certain Primates. *Journ. Mamm.*, Baltimore, Vol. 6, pp. 236–243.

384. WOOD-JONES, F. 1929. *Man's Place Among the Mammals.* Arnold. London.

385. WOODROW, HERBERT. 1928. Temporal Discrimination in the Monkey. *Journ. Comp. Psych.*, Baltimore, Vol. 8, pp. 395–428.

386. WOODROW, HERBERT. 1929. Discrimination by the Monkey of Temporal Sequences of Varying Number of Stimuli. *Journ. Comp. Psych.*, Baltimore, Vol. 9, pp. 123–158.

387. YERKES, R. M. 1907. *The Dancing Mouse.* Macmillan. New York.

388. ——— 1915. Maternal Instinct in a Monkey. *Journ. Anim. Behav.*, Boston, Vol. 5, pp. 403–405.

389. ——— 1916. Ideational Behavior of Monkeys and Apes. *Proc. Nat. Acad. Sci.*, Washington, D.C., Vol. 2, pp. 639–642.

390. ——— 1926. *Almost Human.* Jonathan Cape. London.

391. ——— and LEARNED, B. W. 1925. *Chimpanzee Intelligence and its Vocal Expressions.* Williams & Wilkins. Baltimore.

392. ——— and PETRUNKEVITCH, A. 1925. Studies of Chimpanzee Vision by Ladyginkohts. *Journ. Comp. Psych.*, Baltimore, Vol. 5, pp. 99–108.

393. ——— and CHILD, M. S. 1927. Anthropoid Behavior. *Quart. Rev. Biol.*, Baltimore, Vol. 2, pp. 37–57.

394. ——— and YERKES, D. N. 1928. Concerning Memory in the Chimpanzee. *Journ. Comp. Psych.*, Baltimore, Vol. 8, pp. 237–271.

395. ——— and YERKES, A. W. 1929. *The Great Apes. A Study of Anthropoid Life.* Yale Univ. Press. New Haven.

396. ZUCKERMAN, S. 1929. The Social Life of the Primates. *Realist*, Macmillan, London, Vol. 1, No. 4, pp. 72–88.

397. ——— 1930. The Menstrual Cycle of the Primates.—Part I. General Nature and Homology. *Proc. Zool. Soc.*, London, pp. 691–754.

398. ——— 1931. The Menstrual Cycle of the Primates. Part III. The Alleged Breeding-season of Primates, with Special Reference to the Chacma Baboon (*Papio porcarius*). *Proc. Zool. Soc.*, London, pp. 325–343.

399. ——— 1931. The Menstrual Cycle of the Primates. Part IV. Observations on the Lactation Period. *Proc. Zool. Soc.*, London, pp. 593–602.

400. ——— 1931. The Breeding Seasons of Mammals. (In Preparation.)

401. ZUCKERMAN, S., and PARKES, A. S. 1930. The Oestrous Cycle of the Hamadryas baboon. *Journ. Physiol.*, London, Vol. 69, p. xxxi.

402. ——— 1931. The Menstrual Cycle of the Primates. Part V. The Cycle in the Baboon. *Proc. Zool. Soc.*, London. (In Press.)

INDEX OF ANIMALS

THE following index of the mammalian species mentioned in this book is classified according to the "List of the Vertebrated Animals Exhibited in the Gardens of the Zoological Society of London" (volume on mammals by Major S. S. Flower [111]), and the late Mr. D. G. Elliot's "Review of the Primates" [99].

Class : MAMMALIA

Order I. PRIMATES

Man, the apes, monkeys, tarsius, and lemurs. In this book the term "sub-human primates" has been used in reference only to monkeys and apes.

Family HOMINIDÆ. Man.

Family PONGIDÆ. The anthropoid apes.

Genus GORILLA.
Gorilla gorilla. Gorilla. 12, 45, 93, 160, 173–177, 209, 212, 213, 280, 316
Gorilla beringei. 173
Gorilla rex-pygmæorum. 173

Genus PAN.
Pan satyrus. Chimpanzee. 45, 86, 93, 96–98, 101, 102, 112, 140, 142, 154, 158, 160, 162, 163, 177, 178, 212, 260, 275–291, 294

Genus PONGO.
Pongo pygmæus. Orang Utan. 45, 86, 94, 96, 97, 160, 179, 278

Family HYLOBATIDÆ. The lesser apes.

Genus HYLOBATES.
Hylobates lar (= *H. leuciscus*). Lar gibbon. 23, 46, 86, 94, 160, 179, 180, 212, 303
Hylobates hoolock. Hoolock gibbon. 23, 179

Genus SYMPHALANGUS.
Symphalangus syndactylus. Siamang. 179

Family CERCOPITHECIDÆ. The monkeys. This term can be generally applied to all members of the family, although many have more specific popular names, e.g. langurs, macaques, baboons.

Genus PITHECUS (= SEMNOPITHECUS). 86
Pithecus pileatus. The mitred monkey or capped langur. 303
Pithecus entellus. The entellus langur. 46, 100, 182–183, 213
Pithecus senex (= *Presbytis albinus*). Purple-faced langur. 181
Pithecus obscurus. Dusky langur. 181
Pithecus thomasi. Thomas's langur. 181
Pithecus femoralis. Banded langur. 181
Pithecus johni. Nilgiri langur. 181
Pithecus barbei. Barbe's langur. 181
Pithecus rubicunda. Maroon langur. 182
Pithecus cruciger. Cross-bearing langur. 182
Pithecus chrysomelas. ——. 182

Genus NASALIS.
Nasalis larvatus. Proboscis monkey. 184

Genus COLOBUS. The colobus monkeys or guerezas. 184

Genus CERCOPITHECUS. 87, 143, 184, 301
Cercopithecus pygerythrus. Vervet monkey. 47, 185
Cercopithecus talapoin. Talapoin monkey. 87
Cercopithecus æthiops. Grivet or Abyssinian monkey. 184, 236
Cercopithecus sabæus. Green monkey. 184
Cercopithecus burnetti. Burnett's monkey. 184
Cercopithecus leucampyx stuhlmanni. Stuhlmann's monkey. 184
Cercopithecus albogularis. Sykes' monkey, Mozambique monkey. 185
Cercopithecus samango. Samango monkey. 185.

Genus ERYTHROCEBUS. 87
Erythrocebus patas. Patas or Hussar monkey. 87

Genus CERCOCEBUS. The mangabeys. 143, 186
Cercocebus fuliginosus. Sooty mangabey. 87
Cercocebus collaris. White-collared mangabey. 87
Cercocebus torquatus. White-crowned mangabey. 87
Cercocebus albigena. Grey-cheeked mangabey. 87, 94, 186

Genus MACACA. The macaques.
Macaca radiata. The bonnet monkey. 89, 143, 280

Macaca irus (= *M. cynomolgus*). The common macaque or crab-eating monkey. 48, 89, 100, 143, 188, 215, 235, 299, 306–311
Macaca mulatta (= *M. rhesus*). The Rhesus monkey. 47, 55, 56, 85, 88, 94, 96, 98, 99, 100–106, 111, 139, 140, 143, 146, 156, 187, 215, 235, 269, 299, 306–311
Macaca cyclopis. Formosan or round-faced macaque. 90, 187
Macaca fuscata. Japanese monkey or "ape". 310
Macaca silenus. Lion-tailed monkey. 187
Macaca nemestrina. Pig-tailed macaque. 90, 96, 97, 104, 143, 188, 271–274, 310
Macaca maurus. Moor monkey. 143
Macaca sylvana. Gibraltar or Barbary "ape". Magot. 49, 90, 189, 310

Genus CYNOPITHECUS. Celebes "apes". 91, 190

Genus THEROPITHECUS.
Theropithecus gelada. Gelada baboon. 91, 194

Genus PAPIO. The baboons. 91–93, 99, 209, 212
Papio porcarius. Chacma baboon. 12, 49, 50, 95, 145, 195–207
Papio cynocephalus. Yellow baboon. 49, 195, 236
Papio hamadryas. Hamadryas baboon. 56, 96, 97, 144, 194, 211, 215 *et seq.*
Papio anubis. Anubis baboon. 104

Genus MANDRILLUS.
Mandrillus sphinx. Mandrill. 85, 91, 94, 138, 172, 193
Mandrillus leucophæus. Drill. 95, 172, 193

Family CEBIDÆ. The New World monkeys.

Genus AOTES. Douroucouli or night "ape". 51, 190

Genus CALLICEBUS. Titi monkeys. This name has been applied to the genus SAIMIRI by Wislocki (see p. 209). 190

Genus PITHECIA. Sakis. 190

Genus CHIROPOTES. Sakis. 190

Genus CACAJAO. Uakaris. 190

Genus SAIMIRI. Squirrel monkeys. 51, 191, 209

Genus CEBUS. 160, 191, 208, 209
Cebus apella. Weeper capuchin. 51
Cebus capucina. White-throated capuchin. 51
Cebus azaræ. Azara's capuchin. 51, 191

Genus LAGOTHRIX. Woolly monkeys. 191, 236

Genus ATELES. Spider monkeys. 191, 209, 210
Ateles ater. Black-faced spider monkey. 191
Ateles paniscus. Red-faced spider monkey. 191
Ateles variegatus. Variegated spider monkey. 191
Ateles belzebuth. Long-haired spider monkey. 191
Ateles geoffroyi. Geoffroy's spider monkey. 51, 191

Genus ALOUATTA. Howler monkeys. 192, 209, 210
Alouatta palliata. Mantled howler. 51
Alouatta caraya. Caraya howler. 51, 192
Alouatta seniculus. Red howler. 192

Family HAPALIDÆ.

Genus HAPALE. Marmosets. 51, 141, 190

Family TARSIIDÆ. Tarsius. 48

Family LEMURIDÆ. Lemurs. 66

The general term "lower mammals" has been applied in this book to all mammals other than primates. This has been done for convenience, and the word "lower" is not intended to have any phylogenetic significance.

Order VI. CHIROPTERA

The bats. 36, 64

Order VII. CARNIVORA

Family FELIDÆ.

Genus FELIS.
Felis leo. Lion. 36, 67
Felis onca. Jaguar. 59
Felis catus. Domestic cat. 156–162, 301

Family CANIDÆ.

Genus CANIS.
Canis familiaris. Dog. 72, 73, 74, 101, 109, 110, 114, 121, 122, 124, 156, 159, 164, 165, 238, 280
Canis lupus. Wolf. 292

Genus VULPES.
Vulpes vulpes. Fox. 54, 238

Family MUSTELIDÆ.

Genus PUTORIUS.
Putorius furo. Ferret. 39, 72, 76, 81, 102

Family URSIDÆ.

Genus THALARCTOS.
Thalarctos maritimus. Polar bear. 41

Genus URSUS.
Ursus americanus. American black bear. 35

Order VIII. PINNIPEDIA

Family OTARIIDÆ.

Genus EUMETOPIAS.
Eumetopias stelleri. Californian sea-lion. 29

Family PHOCIDÆ.

Genus HALICHŒRUS.
Halichœrus grypus. Grey seal. 40

Genus PHOCA.
Phoca vitulina. Common seal. 40

Order X. RODENTIA

Family SCIURIDÆ.

Genus SCIURUS.
Sciurus carolinensis. Grey squirrel. 69

Genus CYNOMYS.
Cynomys ludovicianus. Prairie dog or marmot. 23, 63

Genus CITELLUS.
Citellus franklini. Franklin's ground squirrel. 40
Citellus richardsonii. Richardson's ground squirrel. 40

Family MURIDÆ

Genus RATTUS.
Rattus rattus. Rat. 55, 74, 75, 78, 79, 101, 121–125, 128, 130–135, 147, 149, 151, 154, 212, 265–267, 301

Genus MUS.
Mus musculus. Mouse. 74, 101, 104, 119, 134

Genus PEROMYSCUS.
Peromyscus maniculatus gambeli. Deer mouse. 67

Genus APODEMUS.
Apodemus sylvaticus. Long-tailed field mouse. Wood mouse. 38, 43, 67

Genus CLETHRIONOMYS.
Clethrionomys glareolus (= *Evotomys glareolus*). Bank vole. 39

Genus SYNAPTOMYS.
Synaptomys cooperi gossii. Goss' lemming mouse. 67

Family GEOMYIDÆ.

Genus THOMOMYS. Gophers. 59

Family ERETHIZONTIDÆ.

Genus ERETHIZON.
Erethizon dorsatum. Canadian tree porcupine. 59

Family CAVIIDÆ

Genus CAVIA.
Cavia porcellus. Guinea-pig. 78, 80, 101, 119, 125–129, 147, 149, 266–267

Order XI. LAGOMORPHA

Family LEPORIDÆ

Genus ORYCTOLAGUS.
Oryctolagus cuniculus. Rabbit. 59, 72, 76, 78, 81, 118, 119, 123, 126, 127, 129, 133

Order XIV. PERISSODACTYLA

Family EQUIDÆ. Horses. 60, 78

Order XV. ARTIODACTYLA

Family BOVIDÆ.

Genus Bos.
Bos taurus. Domestic ox. 127, 133

Genus Ovis.
Ovis aries. Domestic sheep. 39, 122

Genus Redunca.
Redunca redunca. Reedbuck. 40, 67

Genus Tragelaphus.
Tragelaphus roualigeni. Bushbuck. 40

Family ANTILOCAPRIDÆ.

Genus Antilocapra.
Antilocapra americana. Pronghorned antelope. Prongbuck. 60

Family CERVIDÆ. 69, 234

Genus Axis.
Axis axis. Spotted deer. 25

Genus Cervus.
Cervus elaphus. Red deer. 25

Genus Capreolus.
Capreolus capreolus. Roe deer. 36

Genus Rangifer.
Rangifer tarandus. Reindeer. 41

Family CAMELIDÆ.

Genus Camelus.
Camelus dromedarius. One-humped camel. 34, 126

Genus LAMA
Lama huanacos. Guanaco. 60, 62, 126

Family SUIDÆ. Pigs. 59, 101

Order XX. MARSUPIALIA

Family DASYURIDÆ. Marsupial cats. 130

INDEX OF AUTHORS AND SUBJECTS

NOTE

Some works listed in the bibliography have been cited in the text only by their bibliography numbers, their authors not being mentioned. The numbers of these works are given below in small type against the names of the authors concerned.

Adams, D. K., 158, 159, 160, 170
Akeley, Carl E., 175
Alexander the Great, 7
Allen, Edgar, [9, 13], 89, 99, 100, 102, 103, 105, 108, 109, 139
Allen, J. A., 190, 191, 192, 208
Allen, W. M., 75
Allesch, G. J. von, 260
Alverdes' formula, 21
Alverdes, Fr., 14, 20, 21, 23, 52, 61, 62, 296
American Journal of Mammalogy, 12
Anderson, J., 303
Anecdotes of Simian behaviour, 1–8
Animal psychology—
  history of, 9–11
  relation to sociology, 9, 10
Anœstrous herds, 63
Anœstrus, 33
  effect of on social behaviour, 58–66
Aristotle, 35
Aschemeier, C. R., 177
Associations—
  animal, 52–54
  of primates compared with those of lower mammals, 147
Avery, G. T., 125, 151

Baboon—
  and dead cat, 301
  female born on Monkey Hill, October 1928, 223, 260–262, 274, 275
  killing of young by, 222, 243
Baboons, Hamadryas—
  attitude to sick companions, 263
  attitude to dead, 298–302
  born in captivity, 260, 261
  growth phases of, 223
  "sadistic" attacks of, 227, 243
Bachelors, in Hamadryas baboon colonies, 226
  attachment to family parties, 246, 247
  behaviour of, 248, 249
  fights of, 249, 250
  friendships of, 248
Baker, J. R., [31, 102], 12, 35, 38, 39, 42, 67
Banks, E., 181
Banta, A. M., 128
Barns, T. A., 175
Bartlett, E., 191
Bates, H. W., 190, 192
Bellerby, C. W., [38], 81
Bingham, Harold C., [40], 157, 215, 232, 233, 239, 260, 277–282, 285, 288
Bingham's Chimpanzees, 277–290
Bingley, W., [44], 1–4, 193
Birth-rate of monkeys, variation in, 55, 56
Blair Bell, W., 119
Blanford, W. T., 25, 46, 49, 182, 184, 194
Blyth, E., 182
Bontius, J., 2
Brambell, F. W. R., 38, 119
Brandes, G., 97
Breeding activity—
  classification of, 41

Breeding activity—
continuous,
of Capuchin monkey, 51
of Chacma baboon, 49, 50
of deer mouse, 67
of field mouse, 38, 67
of howler monkey, 51
of lemming mouse, 67
of lion, 36, 67
of lower mammals, 35, 36, 44
of reedbuck, 40, 67
of spider monkey, 51
of sub-human primates, 139
of wood rat, 67
effects of naturalization upon, 41
Breeding season, 32, 33
and society, 53
definition of limits, 42
effect of captivity upon, 36, 37, 41
effect of light upon, 38
effect of low temperature upon, 38
effect of nutrition upon, 39
female, 33
Heape's hypothesis about, 36, 37
male, 33
of American black bear, 35
of bush buck, 40
of Californian sea-lion, 29
of common seal, 40
of grey seal, 40
of ground squirrel, 40
of monkeys and apes, 45–51
of squirrel monkey, 51
physiological changes in male mammal during, 68, 69
relation to animal distribution, 37
teleological explanation of, 34
vocal changes during, 64
Brehm, A. E., 173, 192
Briffault, R., 14, 16, 18, 19, 24, 29, 173
Brown, A. E., 298
Buck, J. L., 177
Buffon, Comte de, 1, 2, 3, 5, 6
Burbridge, B., [57], 174–176
Burton, R. F., 45

Candler, G., 181
Captivity—
effects of upon colony of baboons, 216, 217
records of breeding in, 43, 44
Cercopitheque and dead rat, 301
Chasen, F. N., 189
Chorley, C. W., 175
Christy, C. C., 177
Cole, H. H., [67], 78
Cole, L. W., 154
Collett, R., 181
Collings, M. R., 88, 89
Colony of Hamadryas baboons—
arrangement of, 216
communal behaviour in, 261–263
effects of captivity upon social behaviour in, 216, 217
effects of death of member on, 222
effects of sex-ratio upon stability of, 220
family groups in, 225
in London, constitution of, 211
in Munich, constitution of, 211
in Paris, constitution of, 224
Copulatory antecedents, list of, 281, 282
Corin, J., 14
Corner, G. W., 79, 82, 89, 99, 100, 101, 107, 139
Corpus luteum—
development of, 70
effect upon uterus of monkey, 105
effects upon behaviour, 130
physiological properties of, 79, 80
Crespigny, C. de, 179
Cultural phenomena, relation to physiological events, 19

Cupid and Psyche, 306–311
Cuvier, G., 85

Darwin, C., 9, 36, 62, 64, 65, 85, 138, 142
Dead, retention of by sub-human primates, 298–302
De Haan, J. A. Bierens, 154, 155, 160, 161
De Jongh, S. E., 108
Depredations—
  of baboons in South Africa, 12, 196, 197
  of monkeys, 186, 187
Deschamps, P., 179
De Voss, J. C., 155
Domestication of pig-tailed monkey, 188
Dominance, 233–237, 285, 286
  and socio-sexual relationships, 237
  display of, 270, 271
Drescher, K., 158

Ecology, 11, 12
  correlation with social behaviour, 28, 63
Elliott, D. G., [99], 187, 188
Elliott Smith, G., [97], 25, 149, 153, 154, 169
Elton, C., [102], 12
Endometrium, 71
Ethnology, relation to animal behaviour, 17
Evolutionary succession, principle of and social behaviour, 22, 23
Eyes of lower mammal compared with those of primates, 153

Family of sub-human primate—
  compared with that of lower mammal, 147
  compared with that of man, 315, 316
"Fear-threatening" attitude of monkeys, 228, 251, 294–297
Fee, A. R., [103], 81
Ferocity, alleged, of baboons, 195, 206, 207
Fevold, H. L., 105
Fielding, U., 119
Field-notes—
  on Canadian tree porcupines, 59
  on Chacma baboons, 195–207
  on chimpanzees, 177, 178
  on Gelada baboons, 194, 195
  on gibbons, 179–180
  on gorillas, 173–177
  on guanacos, 60
  on guenons, 184–186
  on Hamadryas baboons, 194
  on jaguars, 59
  on langurs, 181–183
  on macaques, 187–190
  on mangabeys, 186, 187
  on New World monkeys, 190–192
  on orang utans, 179
  on pocket gophers, 59
  on proboscis monkeys, 184
  on prongbuck, 60
  on rabbits, 59
  on seals, 59
  on wild horses, 60
  on wild pigs, 59
  on yellow baboons, 195
Fields, P. E., 154
Firor, W. M., 106
Fischer, J. von, 137, 138
Fish, social responses of, 27
Fitzsimons, F. W., 47, 186, 193, 195, 199, 293
Flea-catching, 57, 58
Flower, S. S., 181, 184, 223
Follicular epithelium, 70
Follicular fluid, 70
Follicular phase, 72, 73
Forbes, H. O., 51, 194
Forbin, 5
Fox, H., [116], 96, 142
Freud, S., 290
Fur, social significance of, 268, 304

Gander, Frank F., [118], 67
Ganson, R., 155
Gardiner, A. D., [102], 12
Garner, R. L., 177, 178
Gear, H. S., 140, 141
Geiling, E. M. K., 106
Gelada baboon, pectoral patch of, 91
Genther, Ida T., 80, 119, 129
Gibraltar apes, history of, 189
Gorilla, reservations for, 12
Grant, C. H. B., 185
Gregariousness of baboons, extent of, 194, 195
Gregg, F. M., 155
Griffith, E., 1, 4
Grinnell, J., [130], 61
Grooming, 57, 58, 144, 148, 201, 202, 226, 227, 230, 240, 243, 248, 254, 257, 258, 259, 261, 263, 270, 272, 299, 301, 304

H., C., 49, 189
Haggerty, M. E., 168, 169, 170
Hamilton, G. V., 139, 140, 215, 232, 238, 299
Hamilton-Smith, C., 1, 4
Hammond, J., [138], 33, 76, 118, 128, 129
Hand movements of monkeys, 156
Harems of baboons—
  formation of, 69
  priority among females in, 226
  temperamental differences between females in, 242–245
Hart, G. H., [67], 78
Hartman, C. G., 55, 56, 94, 96, 98, 101, 102, 106, 109, 111, 112, 139, 140, 269
Heape, W., 35, 36, 37, 39, 40, 46, 47, 86, 96, 100, 118, 127, 128
Hearing of monkeys, 155
Heck, L., 45
Hensel, 192
Herd smell, 63
Hermann, Rudolf, 51
Heuglin, Th. von, 195
Hickson, S. J., 190
Hill, M., [170], [171], 38, 39, 81
Hill, J. P., 130
Hingston, R. W. G., 47
Hisaw, F. L., 105
Hitzheimer, M., 45
Hobhouse, L. T., 164, 165
Hogben, L., 19, 22, 81
Holub, E., 195
Hollister, N., [181], 23, 63
Homosexuality—
  of lower mammals, 130
  of baboons, 229, 230
  of young chimpanzees, 280
  of sub-human primates, contrasted with heterosexuality, 286–289
Hoppius, C. E., 1
Hornaday, W. T., 179, 181, 184
Hose, C., 181
Howard, H. E., 29
Howell, A. B., 64
Howell, C. E., [67], 78
Hughes, T. H., [190], 183
Humboldt, 192
Hume, M., 141
Hunter, W. S., 154, 155
Hunting of Chacma baboons, 199, 204, 205
Hutton, T., 182

Imitation—
  definition of, 167
  of monkeys, 164–171
Implements, use of by monkeys, 159, 160
Insight—
  criterion of, 157, 158
  effects of experience upon, 162, 163
  opposed to trial and error, 161, 162
Intelligence—
  animal, relation to social behaviour, 153

Intelligence—
degrees of, amongst sub-human primates, 160
of cat, 156, 157
of dog, 156, 157
of monkey, 157
Intermixing—
of monkey species, 191, 192
of monkeys and other animals, 195, 206, 207
Investigatory reflexes, 155, 156

Jamison, E., 155
Jenks, A. E., 175
Jerdon, T. C., 182, 187
Joachimovits, R., 90
Johnson, H. M., [203, 206], 154
Johnston, Sir H., 298, 303

Kelaart, F., 181
Kempf, Edward J., 140, 232
Kinder, E. F., 132
Kloss, C. B., 180
Köhler, W., [217], 86, 140, 141, 154, 155, 157, 158, 160–164, 215, 294
Kohts, N., 154–158, 165, 170
Koppenfels, Hugo von, 174
Kroeber, A. L., 26
Kropotkin, P. A., 10, 11

Lactation—
effects of, upon social behaviour, 134, 135
in monkeys and apes, 97, 98
physiological basis of, 133, 134
Lade, Robert, 5
Langley, J. N., 146
Laqueur, E., 108
Lashley, K. S., 238, 269, 273, 274
Learning—
by insight, in lower mammals, 159
by insight, in monkeys, 157
by trial and error in lower mammals, 157
by trial and error in monkeys, 158
Lenz, H., 184
Lindsay, W. L., 9, 10
Loeb, J., 10
Long, F. M., 154
Louttit, C. M., 125, 126, 127, 151, 266, 267
Loveridge, A., 49, 185, 195, 207, 301
Lucas, N. S., 141
Luteal phase, 72, 73
Lydekker, R., 25, 40

Malinowski, B., 14, 15, 29
Marais, E. N., 205, 231
Marcgrave, 4
Marshall, F. H. A., [138], 33, 34, 74, 76, 110
Martius, C. F., 51
Masculine potency, physiological basis of, 68
Masturbatory practices—
of baboons in captivity, 230
of wild baboons, 205
of young chimpanzees, 280
Mating behaviour—
conditioning of, 127
effective stimulus to, in rats, 124, 125
in rats, effects of blindness upon, 123
in guinea-pigs, effects of loss of smell upon, 125
in rats, effects of loss of smell upon, 124
modification of, 151, 152
neuro-muscular mechanism of, 127
of camel, 126
of Chacma baboon, 204, 205
of chimpanzee, 177, 178
of gorilla, 174, 175
of guinea-pig, 125
of llama, 126
of orang utan, 179
of rats, 122, 123
preliminaries to, in baboons, 227
stimuli to, in monkeys, 147

Mating behaviour—
trial and error, in guinea-pigs, 125
McMaster, A. C., 182
McPheeters, C. A., 155
Meeting mechanisms, 66
Memory of sub-human primates, 164
Menstrual cycle—
human, 83
interpretation of, 137
of monkeys and apes, 86–93
problems of, 106, 107
theories of, 107–116
Meyer, R. K., 105
Middleton, A. D., [257], 12
Mid-interval bleeding—
in chimpanzees, 101
in Rhesus macaques, 101
Migration of Chacma baboons, 199
Miller, Gerritt S., 14, 15, 16, 139, 140, 141, 308, 311, 315
Möhnike, O., 45
Monkey Hill—
births on, 222
history of, 218–223
population of, 218, 219
removal of females from, 225
Monœstrous mammals, 72
Monogamy—
of animals, 61
of man, 316
of monkeys, 308–310
Montané, L., 96, 97
Morgan, C. Lloyd, 10
Morgulis, Sergius, 155
Morley, R., 184
Moss, F. A., [267], 55, 127, 151
Mounting of male by female, 228 230
Muir, G. B. F., 187
Müller, S., 45, 179
Munn, N. L., 154
Murie, J., 90
Mutual help of monkeys, 292–294
"blind" character of, 297, 298
Mutual help of monkeys, contrasted with other social relations, 295, 296
relation to dominance, 295

Naturalization—
effect upon breeding habit
of goat, 41
of polar bear, 41
of reindeer, 41
Nelson, E. W., [271], 61
Nelson, W. O., 78, 79
Nesting habits—
of chimpanzee, 177
of gorilla, 174, 176, 177
Northcote, G. A. S., 195
Numbers of baboons, 196–198

O'Donoghue, C. H., 130
Œstrin, 77
effect upon uterus of monkey, 105
extraction of, 77
physiological properties of, 77–79
variation in secretion of, in monkeys, 104, 105
Œstrous behaviour, physiological background of, 119–121
Œstrous cycle, 72
effect upon social behaviour, 117, 118
fundamental plan of, 76
of dog, 73, 74
of ferret, 75, 76
of mouse, 74, 75
of rabbit, 75, 76
of rat, 74, 75
relation to food consumption of rat, 130
relation to muscular activity of rat, 130
relation to nest-building of rat, 130–133
Œstrus, 68, 72
abnormal, definition of, 118
definition of, 118

Œstrus, effect on social habits of baboons, 144, 145
in sexual behaviour of sub-human primates, 139–146
Ogilvie, A. W., 180
Ovarian cycle of baboon, 99–100
Ovarian follicles, 70
Ovarian periodicity, maintenance of, 80
Ovariectomy, effects of, 77
Ovulation, 70
time of, in monkeys, 99
Oxford School of Zoology and Comparative Anatomy, 12
Oxmelin, 4

Pallavicini, 2
Parkes, A. S., [103, 170, 281, 283, 402], 38, 39, 76, 77, 81, 84, 92, 99, 100, 103, 119, 120, 209
Parr, A. E., 27
Pavlov, I. P., 127, 157
Pechuel-Loesche, 186
Pfiffner, J. J., 79
Physiological phenomena, rhythm of, 32
Pidgeon, E., 1, 4
Pig-tailed monkey, sexual relations with her young, 271–274
Pituitary, anterior lobe of—
effects upon œstrous cycle, 80–82
effects upon uterus of monkey, 106
Pocock, R., [287], 86, 87, 89, 90, 91, 138, 141
Polygyny—
animal, 61
effect of dominance upon, 211
effect of sex-ratio upon, 209
in primates, factors underlying, 209
of sub-human primates, 208
Polyœstrous mammals, 72
Pregnancy in monkeys and apes, 95, 96
Presenting, 142, 227, 239
genesis of, 284, 285
of young apes, 275, 276
Primates, evolution of, 24, 25
Promiscuity, absence of among baboons, 228
Pseudo-pregnancy, 72, 73
Puberty in monkeys and apes, 93–95
Pugnacity—
of overlords in baboon colonies, 250, 251
of rutting mammals, 62, 69
of young apes, 276, 277

Reichenow, E., 174, 175
Rennger, J. R., 50, 190, 303
Ridley, H. N., 48, 181, 189
Robertson, D. C., 105
Romanes, G. J., [298], 7, 11, 160
Rowley, J., 30
Russell, B., 159, 163

Sacred monkeys, 182, 187
Saint-Hilaire, Geoffroy, 95, 141
Scent glands, 63–65
of Californian mastiff bat, 64
of primates, 66
Scheffer, T. H., [305], 67
Schipp, Lieut., 7
Schlegel, H., 45, 179
Schultz, A. H., [306, 383], 66
Schuster, L., [307], 36, 40, 67
Schwarz, E., 173
Sclater, P. L., 49, 90, 189
Sclater, W. L., 186
Self-mutilation of monkeys, 308–311
Sentinels, 206
Seton, E. T., [315], 61
Sexual behaviour, development of—
in apes, 275–291
in guinea-pigs, 266, 267
in monkeys, 268–275
in rats, 265–267

Sexual behaviour of monkeys and apes—
and escapes from attacks, 240
and exhibitionism, 232, 281
and friendly advances, 241
and luring of enemies, 240
and movement, 241
and physiological forces, 290
before puberty, 257–259, 276, 279, 282, 284
relation to dominance, 289
relation to that of humans, 15, 290, 311, 312
Sexual dimorphism, effect upon mating habits, 212
"Sexual fights" of baboons, 219, 224, 225, 252–257
Sexuality, diffuse, of monkeys and apes, 238
Sexual prostitution, genesis of, 233, 239, 285, 286
Sexual responses, liberation from strict physiological control, 149–151, 232, 233, 239
Sexual selection, 65
Sexual skin—
and ovulation, 105
changes in, 84, 85
nervous mechanism of, 146
of apes, 86
of baboons, 92, 93
of Celebes "apes", 91
of common macaques, 89, 90
of Formosan rock macaques, 90
of Gelada baboons, 91
of Gibraltar "apes", 90
of guenons, 87
of guerezas, 86
of langurs, 86
of mandrills, 92, 93
of mangabeys, 87
of pig-tailed macaques, 90
of Rhesus macaques, 88
of Talapoin monkeys, 87
physiology of, 102–104
significance of, 137, 138, 146
Sexual stimulus, overriding nature of, 239
Sharpe, Neville A. Dyce, 45, 175, 176
Shaw, Wilfred, 109
Shelford, R. W. C., 179, 188
Shepherd, W. T., [320], 155, 157
Sherrington, C. S., 146
Simpson, G. G., 24
Slack, Dr., 194
Sleeping habits of Chacma baboon, 199–200
Slonaker, J. R., 78, 130, 131, 135
Smell, relation to sexual behaviour of lower mammals, 122
Smith, H. H., 141
Social behaviour—
and individual psychology, 30
and reproductive physiology, 29, 30
plasticity in, 23, 30
Social instinct, 27, 52
Society—
animal, classification of, 20, 52–54
differences between human and animal, 17–26
human, origin of, 26
sub-human primate, 55–58, 212, 213
Sociology—
animal, 10–12
Cartesian compromise in, 19, 20
human, relation to animal behaviour, 12–16
mammalian, subject matter of, 28
Socio-sexual relationships of monkeys—
analysis of, 302, 303
contrasted with those of humans, 312, 313
contrasted with those of lower mammals, 313, 314
permanency of, 311
studies of, 215
Sokolowsky, A., 140, 178

Solitary male monkeys and apes in the wild, 213
Spaeth, R. A., 180
Spencer, H., 13
Spiegel, A., 90, 96, 97, 142
Spix, J. B., 51
Sterndale, R. A., 25, 188
Stevenson-Hamilton, J., 36, 49, 185, 206, 292, 293
Stone, Calvin P., [338, 349], 119, 121, 123, 124, 125, 127, 128, 132, 133, 135, 151, 212, 265, 266, 267
Struthers, P. H., 59, 62
Sturman-Hulbe, Mary, [349], 132, 133, 135
Swinhoe, R., 187, 188

Tavernier, 3
Temperamental differences—
  between females in baboon harems, 242–245
  between young chimpanzees, 278, 279
Terns, behaviour of, 238, 239
Territory of Chacma baboons, 198
Thomson, G. M., 41
Thorndike, E. L., 10, 156–159, 164, 165
Tickell, S. R., 46, 180
Tinklepaugh, O. L., [360], 86, 93, 101, 142, 164, 269, 306–310
Tolman, E. C., 161
Trendelenburg, W., 158
Tsai, Chiao, [362], 55

Uterine cycle, 71
  in monkeys, 100, 101

Vaginal cycle, 71
  in monkeys, 101
Valentine, Willard L., 154
Van Campenhout, E., [360], 86, 93, 101
Van Herwerden, M., 48, 100
Vision—
  colour, 155
  of primates compared with that of lower mammals, 154

Wallace, A. R., 45, 179, 192
Warden, C. J., 9, 154, 155
Warner, L. H., [371], 55, 154, 155
Washburn, M. F., 170
Watson, J. B., 57, 166, 167, 168, 170, 269, 273, 274
Watt, H. J., 156
Westermarck, E., 13, 16, 24, 34, 180
Wilbert, R., 45
Wilkie, R., 155
Winwood Reade, W., 45
Wislocki, G. B., [383], 51, 66, 209, 210
Wood-Jones, F., [384], 25
Woodrow, Herbert, 155
Wroughton, R. C., 184

Yerkes, R. M., 299, 300
Yerkes, R. M., and Yerkes, A. W., 8, 93, 97, 154, 155, 158, 159, 165, 167, 168, 170, 173, 176, 177
Yerkes, R. M., and Yerkes, D. N., 164

Zondek, 119